PHYSIOLOGICAL ZOÖLOGY

A Quarterly Journal of Zoölogical Research

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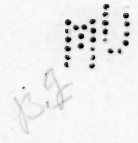

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PHYSIOLOGICAL ZOÖLOGY

Volume XVII JANUARY 1944 Number 1

PHYSIOLOGY OF DEVELOPMENT OF THE FEATHER. VII. AN EXPERIMENTAL STUDY OF INDUCTION[1]

FRANK R. LILLIE AND HSI WANG
Whitman Laboratory, University of Chicago

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I. INTRODUCTION

In the fifth study of this series, which dealt with experimental morphogenesis of the feather (Lillie and Wang, 1941, p. 130), we concluded that "the papilla controls the orientation and general development of the feather either directly or indirectly" by virtue of inductive action of its dermal component[2] on the epidermal cells covering its surface. Indirect evidence led us also to the conclusion that inducing power exists in the form of a bilateral gradient in the entire dorsal half and that the epidermis is totipotent in all

[1] This work was aided in part by a grant from the Dr. Wallace C. and Clara A. Abbott Memorial Fund of the University of Chicago.

[2] Wang (1943) devoted a special study to the respective roles of derma and epidermis and showed that the dermal component of papillae devoid of epidermis possesses full power of induction in either breast or saddle tracts; but that the specific nature of the induced feather, whether breast-type or saddle-type, was a function of the epidermis of the host follicle, so that denuded breast papillae transplanted to saddle follicles produced saddle feathers, and vice versa. Intact breast or saddle papillae, on the other hand, retain specificity in follicles of either tract.

its parts. The result of induction was the establishment of a bilateral "dorsal field" of separate barbs, about fifty in number, beneath the center of which the rhachis arises secondarily. After this we believed that "the ectoderm becomes a self-differentiating system, within which secondary systems governing the mechanism of the development of the feathers arise."

The present paper is an experimental study of the organization and action of the inductor, of the gradients in the collar, and of physiological isolation in the origin of the after-feather, in which the striking results that follow from the new method of grafting inductor and non-inductor parts of donor-papillae to host-papillae are analyzed.

The problem of morphogenetic induction in animals has been studied in recent years exclusively on embryonic stages. It is, therefore, of special interest to find the same principles operative in regeneration of feathers in adult fowl. In embryonic stages both inductor and substratum (the acting and reacting systems of Spemann, 1938, p. 77) are developing systems; but in regeneration of the feather the inductor does not change, and development is confined to the epidermal substratum from which the feather forms. This condition facilitates analysis of inductive action in some respects; the entire developing system is also much simpler than any embryo. Host and graft are parts of the same individual in our experiments, so that questions of compatibility and relative age do not arise to complicate the problems as they do when transplants are made from one embryo to another.

II. TECHNIQUE

The experiments were designed primarily to test the localization, extent, and properties of the inductor. For these purposes the following experiments were made: (1) Portions taken from various locations of donor-papillae were grafted to complete host-papillae in order to test the inducing power of different loci; papillae of breast (B) and of saddle (S) tracts were used both in homologous and in heterologous combinations; (2) the independent powers of reconstitution of portions used as grafts were also tested. Collectively these involved a large number of kinds of experiments ("types"), of which those used in the present communication are recorded, together with their results, in Tables 1 and 2.

All donor-host combinations were autoplastic. Brown Leghorn capons not more than 1 year old were used exclusively; all were castrated in our laboratory at about 2 months of age. The general methods of anesthesia and of operation have previously been described by us (Lillie and Wang, 1941).

The first series of the new experiments, performed in March, 1942, was adapted to test the relative inducing capacity of sectors of mid-dorsal and of mid-ventral origin in both B and S tracts and also between them, making sixteen combinations in all (Fig. 2). These are designated as the "basic experiments" (Table 1, types 1–16). For purposes of further analysis supplementary experiments were made later, first, to test inducing power of other regions and fractions of the papilla and, second, to test the relative power of reconstitution of parts used as grafts (Table 2).

1. THE BASIC EXPERIMENTS (TABLE 1)

The grafting experiments required separate attention for the isolation of the grafts and the preparation of the host-papillae to receive them. Description of the methods used in the basic experiments will suffice for all. The methods used for grafts of dorsal and those of ven-

tral origin are slightly different. In both cases the papillae of regenerating feathers (active papillae) of known age (from 16 to 25 days) were used.

GRAFTS OF DORSAL ORIGIN

Donor-follicles were opened first. Each of their papillae received two longitudinal incisions to the center of the papilla, which isolated the wedge-shaped graft (BD or SD, Table 1) from the remainder of the papilla,[3] and a third (transverse) incision below the base removed the graft from the follicle (Fig. 1).

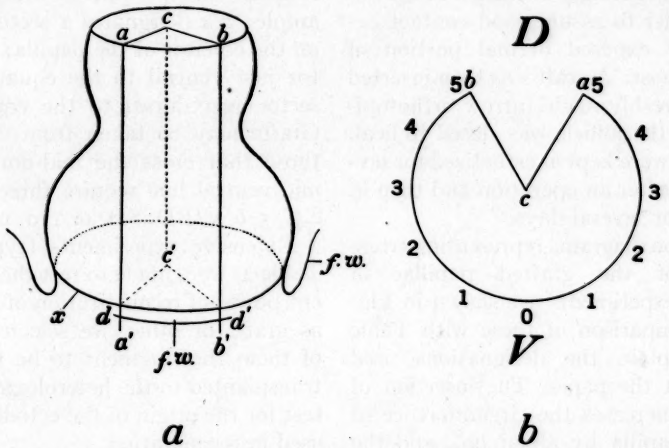

FIG. 1.—Operation diagram, grafts of dorsal origin, BD or SD = sector 5–6–5, Fig. 3 (experiment types 1–8, Table 1). *a*, The papilla viewed as stereogram from the dorsal surface; the wedge-shaped graft is bounded apically by *a*–*b*–*c* and basally by *a'*–*b'*–*c'* carried below the base of the papilla (*x*) to the level *d*–*d'*. *b*, Cross-section of the papilla after removal of the graft; *D*, dorsal; *V*, ventral; *f.w.*, wall of the follicle. 0, 1, 2, 3, 4, 5 explained in Fig. 3, × *ca.* 45.

GRAFTS OF VENTRAL ORIGIN

Grafts of ventral origin, however, could not be obtained in this manner, owing to the concealed position of the ventral surface of the papilla. Instead, the entire ventral half of the papilla was removed and, while in Ringer's solution, was divided by two cuts into three sectors, the two lateral ones of which were then discarded. Both dorsal and ventral grafts were intended to be median sectors, each equivalent to approximately one-sixth of the whole circumference (5–6–5 and 1–0–1, Fig. 3, respectively). It must be admitted, however, that, while it is relatively easy to maintain the uniformity of size of the grafts used in the basic experiments, the absence of any external landmark of the dorsoventral orientation of the papilla introduces a source of error with regard to the precise origin of these grafts, which is reflected to some extent in the results of some of the experiments (p. 7, type 5).

The grafts remained in Ringer's solution until the host-follicles were opened one at a time. The papilla was held below its base by a pair of forceps in such a position that its apex pointed either posteriorly (normal) or anteriorly (reversed). In these two positions the dorsal and ventral surfaces, respectively, of the papilla were exposed for operation.

[3] One of the longitudinal incisions was carried entirely across the papilla, and the other met it in the center.

In either position a longitudinal incision was made on it from base to tip and as deep as the center of the papilla[4] with a tiny scapel made from a piece of watch-spring mounted on a handle. The incision usually injures the central artery and causes the host-papilla to bleed for a minute or longer. The grafting must be done after the bleeding is over and in the absence both of a blood clot within the furrow and of Ringer's solution in the follicle in order to assure good contact between the exposed dermal portion of graft and host. A graft was then inserted into this freshly made furrow orthotopically, and the follicle was closed to heal. The birds were kept anesthetized for several hours after an operation and then in isolation for several days.

Operation diagrams representing cross-sections of the grafted papillae in the basic experiments are shown in Figure 2. Comparison of these with Table 1 will explain the designations used throughout the paper. The insertion of the graft increases the circumference of the host-papilla by about 60°, and the resulting feather cylinder is correspondingly increased to an extent that can readily be recognized by the eye (Pl. VIII, Fig. 27).

2. SUPPLEMENTARY EXPERIMENTS (TABLE 2)

In the supplementary grafting experiments other parts of the papilla than those used in the basic experiments were tested for inducing power by grafting them to mid-ventral positions in host-papilla; they also extend the entire length of the donor-papilla. Both homologous and heterologous combinations were made (types 17–27, Table 2). The parts used (Table 2) will be designated in accordance with Figure 3, which represents a cross-section of a donor-papilla divided into twelve equal sectors (each occupying 30° of the complete circumference), numbered on each side from 0 at the mid-ventral point to 6 at the mid-dorsal point. Since all grafts are sectors with their apexes at the center of the dermal papilla, each kind of graft is represented by two numbers to indicate its location and peripheral width. For example: 2–4 designates a sector centered on the equator of the papilla; 1–3, a sector just ventral to the equator; 3–5, a sector just dorsal to the equator, etc. Grafts may be taken from either side; those that cross the mid-dorsal or the mid-ventral line require three numbers, e.g., 5–6–5 (BD, SD) or 1–0–1 (BV, SV).

Extensive experiments (types 28–39, Table 2) were made to test the independent power of reconstitution of parts used as grafts or otherwise selected. In two of them the fragment to be tested was transplanted to the heterologous tract to test for the origin of the ectodermal cells used in regeneration.

III. TABLES 1 AND 2

1. GENERAL

In the basic experiments 39 per cent, and in the supplementary grafting experiments 57 per cent, of the operated papillae failed either to take the graft or to regenerate. These account for the discrepancy between the number of operated follicles and the number of feathers obtained in Tables 1 and 2. A normal feather showing no effect of the graft is taken as evidence for failure of incorporation and is not recorded in the tables. In case of successful incorporation, regeneration is almost immediately resumed without appreciable delay in emergence as compared with controls plucked at the time of operation. On the other hand, regeneration of isolated

[4] Here a second possible source of error is introduced. Just as the grafts may deviate from the intended median sector, so the longitudinal incisions might occasionally miss their exact mark for the same reason.

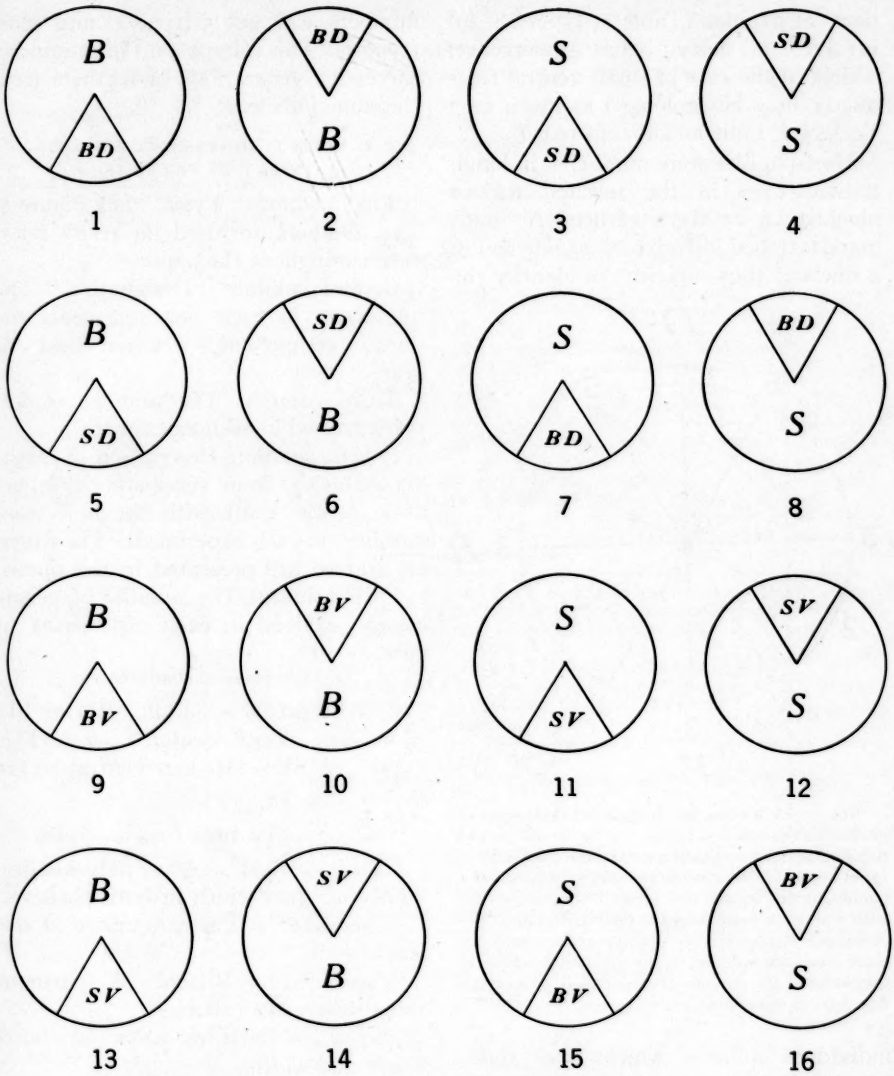

FIG. 2.—Composition diagrams of the basic experiments (Table 1) shown in cross-section. B = breast, S = saddle. The wedge-shaped grafts are designated by two letters: BD and BV, sectors of breast papillae of dorsal (5–6–5, Fig. 3) and ventral (1–0–1) origin, respectively; SD and SV, similar sectors of saddle papillae. 1–8, representing experiment types 1–8 (Table 1), show grafts of dorsal origin; 9–16 (Table 1) show those of ventral origin. 1, 2, 3, 4, 9, 10, 11, 12 are homologous combinations; 5, 6, 7, 8, 13, 14, 15, 16 are heterologous combinations. In all cases, since the host is a complete papilla, the addition of the graft increases the total circumference by about 60°, both of the papilla and of the feather cylinder developed from it (cf. Pl. VIII).

parts of papillae (Table 2, types 28–39) involves a delay before emergence, which, in the case of small ventral fragments, may be prolonged as much as 3 weeks (cf. Lillie and Wang, 1941).

Host-papillae were numbered in longitudinal rows in the selected regions plucked 16–25 days earlier. A single mark tattooed in India ink at one end of a row was thus sufficient to identify the individual follicles which were numbered consecutively for each experiment. Usually two different types of experiments, though bearing one book number, were performed simultaneously on one bird; subnumbers used for individual follicles run continuously for both types (e.g., Expt. 406:1–7, type 1; Expt. 406:8–12, type 3; Table 1). Individual feathers are accordingly identified by two numbers, e.g., 406:5 (type 1) and 406:8 (type 3). This is important in comparing successive generations of feathers from the same follicle.

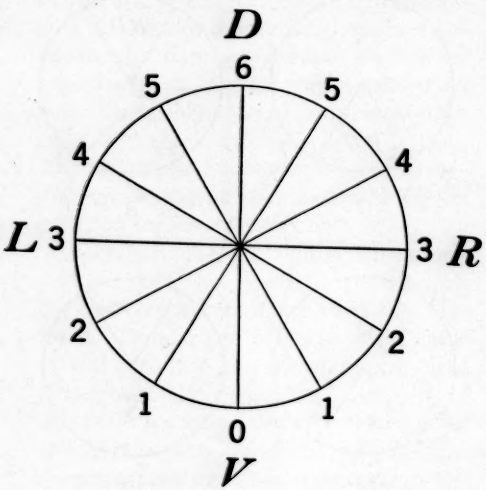

FIG. 3.—A scheme for designating derivation of grafts (Tables 1 and 2, types 1–27) or of portions of papillae used in reconstitution experiments (Table 2, types 28–39). It represents a transverse section of a papilla divided equally into six sectors on either side, with 0 and 6 representing the mid-ventral and mid-dorsal points, respectively. Each part designated by these numbers extends in the form of a wedge to the center of the papilla. *D* = dorsal; *V* = ventral; *L* = left; *R* = right.

2. TABLE 1: THE BASIC EXPERIMENTS (TYPES 1–16, FIGURE 2)

First column: "Type." See Figure 2. The numbers are used for ready reference throughout the paper.

Second column: "Designation." The numerator in each case represents the dorsal component, whether host or graft.

Third column: The number of follicles grafted in each experiment.

Fourth column: Description of feathers resulting from successful incorporation of the graft with the individual numbers in each experiment. The feathers starred are presented in the plates.

Fifth column: The number of generations obtained in each experiment to date.

ABBREVIATIONS (SECOND COLUMN)

B = Breast, S = Saddle; BD or SD = Median dorsal sector (5–6–5, Fig. 3); BV or SV = Median ventral sector (1–0–1, Fig. 3).

TERMINOLOGY FOR TWINS (FOURTH COLUMN)

"Asymmetrical" = Vane-halves of distinctly unequal width in both partners.

"Complete" = Partners united at the calamus.

"Conjoined" = Rhachi of partners united above the calamus.

"Equal" = Partners alike in both length and width.

"Symmetrical" = Vane-halves of approximately the same width in both partners.

3. TABLE 2. THE SUPPLEMENTARY EXPERIMENTS (TYPES 17–39)

A. THE GRAFTING EXPERIMENTS

In all cases the grafts are placed in a mid-ventral position in the host papilla.

TABLE 1

THE BASIC EXPERIMENTS

Experiments		No. Follicles Operated	Feathers Obtained	No. Generations Obtained
Type	Designation			
1.....	B/BD	14	5 twins complete and equal, face to face, symmetrical or nearly so (403: 10*, 14*; 406: 1, 5, 7; Pl. I, Fig. 12; Pl. VIII); 3 of them without after-feathers, 2 pairs have one each 1 conjoined twin (403: 9)	5 in 403 1 in 406
2.....	BD/B	5	1 triplet (412: 8*, Pl. III, Fig. 17) 3 twins, equal in length, asymmetrical, mirrored, and conjoined (412: 6*, 7, 9; Pl. III, Fig. 18); no after-feather in 6 and 9, one in 7 1 single feather with widened half-vane on right (No. 10)	1
3.....	S/SD	12	2 twins, complete and equal (406: 8, 10; feathers lost on bird) 1 twin, complete and equal in length, one partner narrower (404: 10*, Pl. II, Fig. 14); no after-feather	1 in 406 3 in 404
4.....	SD/S	5	2 twins (413: 2, 4): No. 4 complete and equal; No. 2 one partner shorter; no after-feather	1
5.....	B/SD	15	5 twins (407: 1, 2, 3, 4*, 6; Pl. II, Fig. 15), equal in length and complete. In all cases host partner B, donor-partner a typical transverse chimaera; 2 after-feathers in No. 2, one in No. 6, absent in others (Experiment 403: 5 twins and 3 single feathers; both partners and singles with chimaera characters, but variable; these results can be explained by deviations in the operation; cf. p. 3, "Technique")	2 in 407 4 in 403
6.....	SD/B	8	1 triplet (401: 5*, Pl. III, Fig. 19) 2 twins (401: 3, 6), partners are chimaerae, complete, but unequal in length 1 single feather, a chimaera (No. 4); no after-feathers	4
7.....	S/BD	15	10 twins, complete and equal in length (404: 1–8 incl.: 408: 8, 10*; Pl. II, Fig. 16); in all, host-partner pure S, donor-partner a typical longitudinal chimaera; after-feathers absent in all except a single one in 404: 8	2 in 408 3 in 404
8.....	BD/S	11	8 twins (402: 3, 4, 5, 6; 409: 1, 3, 4, 5) all conjoined, side by side, equal in length. If the graft is lost, both partners are pure S (402: 3); if it persists, its material is distributed so as to produce variable chimaera characters in one or both partners 1 single pseudobilateral chimaera (409: 2); one after-feather present in 402: 3 and 409: 1 and 2; absent in others	3 in both 402 and 409
9.....	B/BV	15	9 single feathers affected by graft: in two (412: 3, 5) the barbs of the fluff are elongated, after-feather normal; in seven (412: 1* and 412*a*: 1, 2, 3, 4, 8, 9) the after-feather is enlarged and elongated (Pl. V, Fig. 22)	1 in both 412 and 412*a*

TABLE 1—*Continued*

Experiments		No. Follicles Operated	Feathers Obtained	No. Generations Obtained
Type	Designation			
10.....	BV/B	15	A. 10 twins (405: 7, 8, 9*; 405*a:* 1, 3, 4, 6, 7, 8, 9): two are complete, equal, and symmetrical (Pl. IV, Fig. 20); the others are either complete or conjoined, and one partner is shorter. All pairs rotated about 90° on their long axis when on the bird. After-feathers: two in 405: 9, four pairs have one each and four have none B. 1 single feather (405: 6*) with a huge after-feather (Pl. V, Fig. 23)	2 in both 405 and 405*a*
11.....	S/SV	10	4 single feathers with enlarged after-feather (413: 1*, 2, 3, 4; Pl. VI, Fig. 24)	1
12.....	SV/S	15	3 twins (409*a:* 2, 3, 4), complete and equal, symmetrical, rotated as in type 10; one after-feather in Nos. 2 and 3, none in No. 4 6 single feathers with multiple after-feathers (409: 6, 7, 9; 409*a:* 6, 7, 8) 1 single feather with elongated fluff barbs (409*a:* 9)	2 in both 409 and 409*a*
13.....	B/SV	7	6 single B feathers with enlarged, single or multiple after-feathers (407: 8, 9, 10, 11, 12, 14)	2
13*a*.....	B/S (3–0–3)	10	8 single B feathers with enlarged, single or multiple after-feathers (407*a;* 2, 3, 4, 5, 7, 8*, 9, 10): No. 8 has five after-feathers (Pl. VII, Fig. 26)	2
14.....	SV/B	11	5 Twins (401: 9, 10*, 12; 405: 2, 4): three cases: complete, equal, or subequal, with chimaera characters on inner vanes and no after-feather (Pl. IV, Fig. 21); one similar but conjoined; one with both partners pure B owing to loss of graft 2 single chimaerae (405: 1, 3)	4 in 401 2 in 405
15.....	S/BV	6	4 single feathers (408: 2, 3, 4, 5) with one half-vane S, the other half-vane a transverse chimaera: two have enlarged after-feathers, two half-vane after-feathers	2
16.....	BV/S	9	5 twins (414: 1, 2, 4, 5, 7), complete or conjoined, equal or unequal: four with chimaera characters, two with after-feathers 2 single feathers with enlarged after-feather and higher fluff-level on right (402: 8*, 9; Pl. VI, Fig. 25)	3

First column: As in Table 1.

Second to fifth columns: As in Table 1, except that in the second column the designation of the grafts follows the system of Figure 3 (p. 6).

Terminology: As in Table 1.

Types 17–19: S grafts to B hosts.

Types 20–23: B grafts to B hosts.

Types 24–27: S grafts to S hosts.

B. RECONSTITUTION EXPERIMENTS (TYPES 28–39)

Parts of papillae developing independently, to be identified by reference to Figure 3. Columns as in Table 2, *A*.

IV. RELATIVE INDUCING POWER OF PORTIONS OF THE PAPILLA

The method of measuring inducing power is to test various portions of donor-

TABLE 2

SUPPLEMENTARY EXPERIMENTS

Experiments		No. Follicles Operated	Feathers Obtained	No. Generations Obtained
Type	Designation			
	A. Grafting Experiments			
17.....	B/S(1½–4½)	10	3 single B feathers with enlarged after-feather (504: 1, 2, 4); with widened fluff on left (No. 3)	2
18.....	B/S(1–3)	12	3 single B feathers with unilateral S margin and normal after-feather (506: 1, 2, 3)	2
19.....	B/S(0–3)	14	9 single B feathers with S margin and enlarged after-feathers (502: 1–9 incl.)	3
20.....	B/B(3–5)	10	3 unequal twins (603: 1, 2*, 8) with donor-partner short and defective; after-feather single or missing (Pl. I, Fig. 13) 1 single feather with a huge half-vane after-feather (No. 4)	2
21.....	B/B(2–4)	8	1 single feather (604: 11) with profuse after-feather, and elongated barbs in fluff, right side	2
22.....	B/B(1½–4½)	21	3 twins (605: 1, 16, 17) with one partner half-vane 4 twins (605–6: 2, 5, 10, 12), conjoined but not quite equal in length, asymmetrical, and mirrored 1 twin (No. 3), complete and equal 2 single feathers (Nos. 11, 20) with enlarged after-feathers (exceptions)	2
23.....	B/B(1–3)	10	9 single feathers with enlarged after-feathers: two each (609–10: 1, 4, 5, 7, 9); one (Nos. 3, 6, 8); one with half-vane in fluff and normal after-feather (No. 2) 1 twin (No. 10), unequal, complete, with one after-feather (exception)	2
24.....	S/S(3–5)	10	3 unequal twins (601: 9, 11, 13)	1
25.....	S/S(2–4)	7	1 twin (602: 7), partners equal in length, but donor-partner weaker	1
26.....	S/S(1½–4½)	19	3 unequal twins (607–8: 5, 9, 18), conjoined or complete 1 twin (No. 17), complete and equal 2 single feathers (Nos. 1, 4): one with a half-vane fluff, the other with elongated barbs in fluff right side	1
27.....	S/S(1–3)	16	9 single feathers: with enlarged after-feather or increased length of barbs in fluff (611–12: 2, 5, 9, 10, 14); with two after-feathers (Nos. 4, 6, 8, 12)	1
	B. Reconstitution Experiments			
28.....	B(5–6–5) *in situ*	6	5 single feathers, normal but with minor defects (514*a*: 1–5 incl.); no after-feathers	2
28*a*.....	B(5–6–5) transplanted to S follicle	12	5 single chimaera feathers, size equal to normal (515*b*: 4, 6, 8, 9, 10); after-feather present in three of them 1 normal B feather (No. 3) 1 asymmetrical (No. 5)	2

TABLE 2—*Continued*

Experiments		No. Follicles Operated	Feathers Obtained	No. Generations Obtained
Type	Designation			
29.....	S(5–6–5) *in situ*	12	4 single feathers (515*a*: 2, 4, 7, 9) narrower, weaker than normal; no after-feathers; fluff reduced	2
29*a*.....	S(5–6–5) transplanted to B follicle	9	2 single feathers (514*b*: 2, 5) similar to type 29; no chimaera characters; no after-feather 1 tuft feather (No. 4) 1 defective feather (No. 6); no after-feather	2
30.....	B(3–6) *in situ*	10	7 single feathers (with asymmetrical vanes), normal length but weaker than normal (701: 1, 3, 4, 5, 7, 8, 9); no after-feathers	2
31.....	S(3–6) *in situ*	16	8 single feathers varying from approximately normal (704: 1, 14) to shorter, narrower with asymmetrical vanes (Nos. 4, 9, 11, 13, 15, 16); no after-feather	2
32.....	B($1\frac{1}{2}$–$4\frac{1}{2}$) *in situ*	22	6 half-vane feathers (702–3: 10, 13, 14, 17, 24, 27): half of them with an after-feather 3 single feathers with asymmetrical vanes (Nos. 16, 19, 22) 1 weak bilateral B feather without an apex (No. 28)	2
33.....	S($1\frac{1}{2}$–$4\frac{1}{2}$)	37	5 half-vane feathers (705–6: 21, 24, 44, 47, 50): after-feather absent except in No. 50 5 tuft feathers (Nos. 27, 29, 30, 43, 49) 4 bilateral feathers with defective apexes (Nos. 23, 28, 52, 53)	2
34.....	B(1–0–1) *in situ*	15	6 very small tuft feathers (710: 1, 3, 6, 7, 8, 11)	1
35.....	S(1–0–1) *in situ*	25	9 very small tuft feathers (711: 5, 8, 10, 13, 14; 504: 3, 5, 6, 8)	1
36.....	B(3–0–3) *in situ*	36	From 1941 paper: 21 half-vane feathers, 2 bilateral, and 10 tuft feathers	3
37.....	S(3–0–3) *in situ*	25	11 half-vane feathers (707: 1, 2, 3, 4, 5, 7, 8, 9, 11, 15, 20); after-feather present 7 tuft feathers (Nos. 6, 16, 17, 21, 22, 24, 25) 2 bilateral feathers with defective apexes (Nos. 10, 14); after-feather present	2
38.....	B($1\frac{1}{2}L$–0–$4\frac{1}{2}R$) R-inclined	32	12 half-vane feathers (right-sided: 801: 1, 5, 11, 12, 13, 17, 25; left-sided: Nos. 7, 8, 15, 19, 22) 2 tuft feathers (Nos. 3, 20) 15 bilateral feathers, of which 7 have apical defects (see text, p. 18); after-feather present in both bilateral and half-vane feathers	2
39.....	B($1\frac{1}{2}R$–0–$4\frac{1}{2}L$) L-inclined	26	11 half-vane feathers (left-sided: 802: 1, 2, 4, 10, 12, 16, 19, 20; right-sided: Nos. 6, 15, 18) 4 tuft feather (Nos. 5, 11, 13, 14) 6 bilateral feathers, of which 2 have apical defects; after-feather present in both bilateral and half-vane feathers	2

papillae against the host-inductor by grafting to a mid-ventral incision in the host-papilla; this is as far as possible from the host-inductor. If a feather is induced by the graft, its length in comparison with that of the host-feather is a measure of the time of induction, on the principle that all parts of the feather

cylinder grow at the same rate (Juhn and Fraps, 1936; Fraps and Juhn, 1936; Lillie, 1940). Length is accepted as the best index of power of induction; but it is also true that the degree of perfection of the feather induced by the graft is proportional to the time of induction; this is, however, not readily measured.

In such tests of inducing power the assumptions are that host- and donor-inductors have equal chances in the competition for control of the substratum (epidermis) and that parts used as grafts retain their original inductive power.[5] In normal regeneration of feathers the first evidence of induction in the epidermis does not appear earlier than the fourth day after plucking, which gives plenty of time for incorporation of the donor-inductor before the host-inductor operates; and the fact that in twins the strongest donor-induced partners are equal in length, and in the homologous combinations B/BD and S/SD (Pl. I, Fig. 12; Pl. II, Fig. 14) in most other respects also, to the host-partners justifies the assumptions.

The basic experiments (Sec. V) demonstrate that a mid-dorsal sector comprising about 60° of the circumference of the papilla possesses full inducing power and that a mid-ventral sector is devoid of inducing power. The supplementary experiments (Table 2, *A*) were made for the purpose of determining boundaries and gradations between these regions. Power of induction is a relative term which comprises an unmistakable maximum but grades off to a minimum where the autonomous power of development exhibited by the after-feather may even appear to overlap it. Whether or not there is a sharp distinction between minimum inductive power and autonomous power of development is discussed later (see p. 22).

[5] In such sectors, however, the inducing power is limited to the more basal portion. If the complete sector BD (5–6–5) is divided into an apical and a basal half, it is found that, used as grafts in a mid-ventral position of a host-papilla, the basal half has power of induction practically equal to that of the entire sector, whereas the apical half has no power of induction but behaves like a ventral sector. This agrees with Foulks's recent interpretation (1943) that an extensive portion of the apex of the dermal component of the papilla is essentially residue of the pulp of the preceding generation of the feather. An additional difference between basal and apical portions is that, when reimplanted in an empty follicle, the former develops into a practically normal feather, but the latter does not form a feather.

V. THE BASIC EXPERIMENTS (TYPES 1–16)

We designate types 1–16 (Fig. 2 and Table 1) the basic experiments because they were the first performed and are also the most systematic. They bring up most of the problems with which the other types of experiments (17–39), designated as "supplementary" (Sec. VI), deal. We shall treat the grafts of mid-dorsal origin (types 1–8) and those of mid-ventral origin (types 9–16) separately.

For each type of experiment we shall select for description the specimens that give the most typical result; in some experiments (e.g., types 2, 6, 10) two results may be classed as typical, depending on slight variations in placing the graft. The criterion is uniqueness of the result, supplemented by its frequency. Results that depart more or less from the typical are included in the tables, but often not in the text. Reasons for such departures have been considered already in the section on technique.

1. THE EFFECTS OF GRAFTS OF MID-DORSAL ORIGIN, BD AND SD (TYPES 1–8)

The grafts represent the sector 5–6–5 in Figure 3. The results fall into two groups: (*A*) the grafts placed ventrally in the host-papilla; (*B*) the grafts placed dorsally.

A. PLACED VENTRALLY (TYPES 1, 3, 5, 7)

Ventral placement of the graft is the best and simplest test of inductive power, for it is at the greatest possible distance from the inductor of the host, and interferences are thus avoided for the longest possible period of time. It is to be noted that two of the types (viz., 1 and 3) are homologous combinations, i.e., both host and donor from breast papillae (1) or both from saddle papillae (3); and the other two are heterologous combinations, the host B and the graft S (B/SD) in 5, and host S and graft B (S/BD) in 7. Both kinds of combination have certain advantages in interpretation of results.

a) *The homologous combinations.*—In the best cases twins of equal length with ventral surfaces apposed, united only in a common calamus, are formed (Pl. I, Fig. 12; and Pl. II, Fig. 14). In the B combination (type 1) one of the twins, presumed to be the one induced by the graft, exhibits minor defects, owing to imperfect union of host and graft. Otherwise the partners are alike. In the S combination (type 3), in the specimen shown (Expt. 404), one partner is narrower than the other, but in two other specimens (Expt. 406) this was not the case. Twins of both combinations are usually without after-feathers, though one of the partners may possess one.

This result demonstrates that the isolated and transplanted graft has inductive power equal to that of the complete inductor of the host, for it controls, directly or indirectly, half of the epidermis of the combined papilla, as illustrated in Figure 4, *a*. "Ventral" triangles are formed equidistant from the two rhachi. Epidermis that had the prospective potency of the ventral half of the feather cylinder, i.e., the distal segments of barbs, has formed complete barbs under the influence of the graft-inductor; the prospective potencies of the dorsal half of the feather cylinder with regard to levels of barbs have also been transformed. All parts of the epidermis of the papilla are therefore totipotent with reference to the regeneration of the barbs—a conclusion that is repeatedly substantiated by other experiments.

b) *The heterologous combinations* (*types 5 and 7*).—These combinations have the advantage over the homologous combinations in that they prove directly the participation of the graft-epidermis by the appearance of chimaera characters in the ventral partner. The substantial equality in length of the host-induced and the graft-induced partners (Pl. II, Figs. 15 and 16) demonstrates that the inductors of the host and of the graft have acted nearly simultaneously. The fact that the graft-induced partner is a chimaera shows that the control of the graft extends into the epidermis of the host; the B graft, however, controls more of the host epidermis than the S graft, judging from the relative widths of the respective partners. The triangles of the B/SD combinations have therefore formed a little below the equator of the conjoined cylinder and those of the S/BD combinations a little above the equator, as shown in Figure 4, *b* and *c* (cf. p. 26).

Another feature to be observed is that the chimaera produced in the B/SD combination is a transverse chimaera (Pl. II, Fig. 15) and that the reciprocal S/BD (Pl. II, Fig. 16) is a longitudinal chimaera. This is in accord with our previous determination (Lillie and Wang, 1943) that, in a chimaera collar, B epidermis gradually displaces S in the direction of tangential movement of the barbs but that S epidermis does not have this power over B. The ventral partners of the two heterologous combinations represent these two conditions.

B. GRAFTS OF MID-DORSAL ORIGIN PLACED DORSALLY (TYPES 2, 4, 6, 8)

In these operations the host-inductor is divided in its center for insertion of the graft (Fig. 5, *a*). Thus three centers of induction may be established dorsally: the graft-inductor and the right and left halves of the host-inductor; in the latter the centers of induction, for reasons to be discussed separately (p. 23), are displaced toward the equator. More usually, however, only two of the centers of induction function. This is frequently due to eccentric placing of the graft (Fig. 5, *b*). Here again we distinguish homologous (2 and 4) and heterologous (6 and 8) combinations.

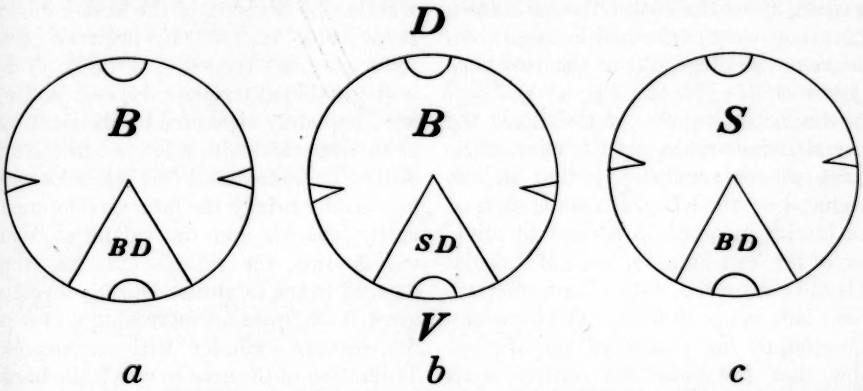

FIG. 4.—Diagrams of relative inducing power of BD (5–6–5) and SD (5–6–5) grafts. *a* = BD against B (the same diagram would serve for SD against S); *b* = SD against B; *c* = BD against S. The position of the triangles indicates the proportion of the substratum controlled by each inductor: equal in *a*, B or BD dominating in *b* and *c* (compare Pl. I, Fig. 12, for *a;* Pl. II, Fig. 15, for *b;* and Pl. II, Fig. 16, for *c*).

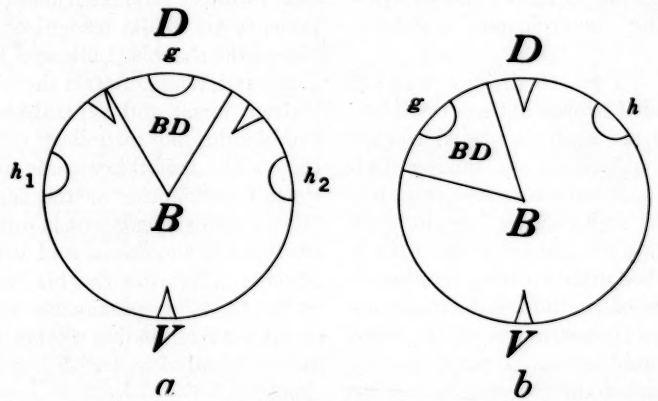

FIG. 5.—Diagrams illustrating different results from grafts of dorsal origin placed dorsally (Table 1, type 2; cf. types 4, 6, 8). *a*, The graft splits the host-inductor equally, resulting in triplets from 3 functional inductors (Pl. III, Figs. 17 and 19), the donor-inductor and the two halves of the host-inductor; *g*, h_1, and h_2 represent the positions of the rhachi of the graft-induced and host-induced partners, respectively. *b*, Graft placed eccentrically at one side of the host-inductor, resulting in conjoined twins with rhachi close together and asymmetrical vanes in both partners (Pl. III, Fig. 18). The triangles in *a* and *b* mark the limits of control of the inductors.

a) *Triplets.*—One triplet was pro-

duced out of five operations in type 2 (BD/B) and one out of six operations in type 6 (SD/B). It is to be noted that no triplets were produced in types 4 and 8, in which S was the host, although sixteen operations were performed in these combinations. Photographs of the two triplets are shown (Pl. III, Fig. 17 and 19). In the heterologous combinations the central member has only S characters, which proves conclusively that it was produced by the SD graft, while each of the lateral members produced by division of the host-inductor has a B rhachis, as is to be expected, with S barbs on part of one side in one of them. The locations of union of the rhachi of the triplets show that the induction centers were close together (Fig. 5, *a*). The condition is not stable, and the median partner disappears in the second and third generations, though the S epidermis still persists in the heterologous combination.

b) *Twins.*—Two conditions lead to twins instead of triplets in these combinations: (1) if the graft is placed too far laterally, it suppresses the smaller division of the host-inductor, resulting in a graft-induced and a single host-induced feather (Fig. 5, *b*), and (2) if the graft is lost or resorbed after insuring separation of the halves of the host-inductor, both twin-partners are host-induced. The heterologous combinations (types 6 and 8) serve to diagnose the two conditions, for in the first case one partner (or both) will be a chimaera, but not so in the second case. Both conditions are recorded in Table 1 (types 6 and 8).

c) *General.*—The results from grafts of mid-dorsal origin placed dorsally confirm the conclusions derived from their ventral placement as to their inducing power and introduce a number of special problems, of which the displacement of the centers of induction of the host toward the equator is the chief one (p. 23).

The various types of twins produced by the experiments (cf. also p. 16), whether by division of the host-inductor (types 2, 4, 10, etc.), by presence of an inductor graft (types 1, 3, etc.), or by both combined (triplets, types 2 and 6), are completely explained by the locations of the inductors with reference to one another. To understand this it is necessary to consider briefly the later development of the rhachis and the calamus. As is well known, the rhachis enlarges from its apex to the calamus. During development it occupies an increasing sector of the feather cylinder with consequent diminution of the area in which the barbs form and grow. Finally, the barb area is completely eliminated at the superior umbilicus. Apart from the barb petioles that form the lateral surfaces, three components are to be recognized in formation of the rhachis (Lillie and Juhn, 1938; Lillie and Wang, 1941): the highly keratinized dorsal and ventral surfaces and the bladder-like medullary cells between them. The medullary component of the rhachis terminates at the superior umbilicus, and the calamus is formed exclusively from the dorsal and ventral components. The after-rhachis behaves similarly to a proportionate extent and forms a corresponding section of the calamus smoothly fused with the larger portion.

Two rhachi situated 180° apart in the feather cylinder meet only in the calamus (B/BD, S/SD, B/SD, S/BD—types 1, 3, 5, 7, respectively). If the two rhachi are closer to each other, they will naturally unite earlier on the short side, producing conjoined twins, and the rhachis formed by their union will then proceed as a unit. The level of union will be determined by the angular distance that separated them originally.

2. THE EFFECTS OF GRAFTS OF MID-VENTRAL ORIGIN, BV AND SV, I–O–I (TYPES 9–16)

The results to be described show that grafts of mid-ventral origin have no inducing capacity; in this respect they contrast in a most positive manner with grafts of mid-dorsal origin and thus serve as controls of the properties of the latter. Exactly the same types of experiments in equal numbers were performed with grafts of mid-ventral as with those of mid-dorsal origin, and the contrasts are confirmed at every point. Nevertheless, positive results of their own kind and of great interest are produced.

A. PLACED VENTRALLY (TYPES 9, 11, 13, 15)

As the graft placed ventrally (Fig. 6, *a*) increases the peripheral distance from the rhachis to the center of the ventral hemisphere, it might be anticipated a priori that the extra distance would be added to the length of the barbs; this happens occasionally. On the other hand, if the range of control of induced gradients in the collar (p. 25) is not adequate to include additional material, the latter would be added to the material that normally forms the after-feather. The latter condition is usually realized (cf. Fig. 10, *e*).

A striking example derived from B/BV (type 9) is shown in Plate V, Figure 22. This specimen has an extraordinarily large after-feather with its own rhachis and barbs that have vanelike apexes. The length of the after-feather shows that it acquired independence when only about half of the vane of the main feather was formed. In the normal breast feather the after-feather does not begin to form until all of the vane and half of the fluff of the main feather is formed. Thus the added ventral material has not only caused the formation of an extra-large after-feather but has also accelerated the time of its origin. This result is typical of the addition of ventral material to the host, even in some cases when it is placed dorsally (cf. Sec. B, below). A much less striking case of

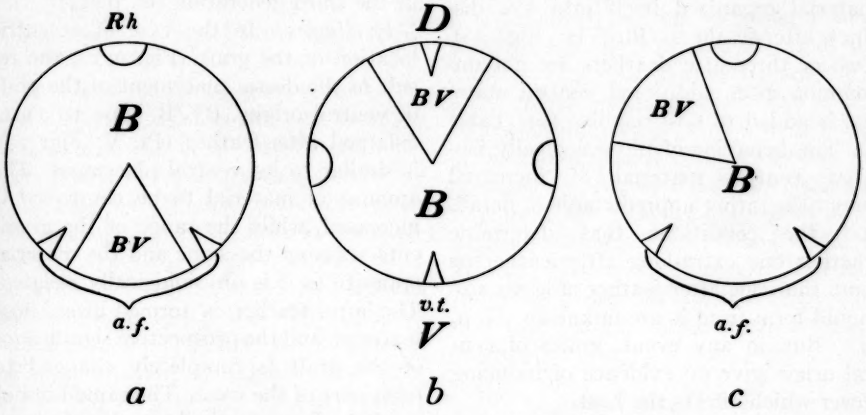

FIG. 6.—Diagrams illustrating different results from grafts of ventral origin (Table 1, cf. types 9 and 10). *a*, When placed ventrally, the graft merely increases the size and length of the after-feather (Pl. V, Fig. 22, and cf. text fig. 10, *e*). When placed dorsally, two different conditions may occur. *b*, The graft divides the host-inductor in two, resulting in complete and equal twins (Pl. IV, Fig. 20). *c*, The graft located beside the host-inductor yields the same end result as in *a*, i.e., an enlarged after-feather (Pl. V, Fig. 23). *a.f.* = after-feather; *v.t.* = ventral triangle; *Rh* = rhachis.

an enlarged after-feather is shown in the combinations S/SV (type 11, Pl. VI, Fig. 24).

The heterologous combinations (types 13 and 15) do not, as such, add anything to the results from homologous combinations. However, in a special type of experiment (Table 1, 13*a*) an entire ventral half of an S papilla, three times the usual amount, was added ventrally to a B host. In one specimen (407*a*:8) the excess material organized itself into five distinct after-feathers (Pl. VII, Fig. 26). Two or three after-feathers are not uncommon after additional ventral material is added to host-papillae (see Table 1). The behavior of physiologically isolated ventral material of increased amount is rather unpredictable in detail, and the conditions that determine whether one extra-long after-feather or more than one after-feather of lesser size should form from it are unknown (cf. p. 27). But, in any event, grafts of ventral origin give no evidence of inducing power which affects the host.

B. GRAFTS OF MID-VENTRAL ORIGIN PLACED DORSALLY (TYPES 10, 12, 14, 16)

Like grafts of mid-dorsal origin placed dorsally, these operations begin by division of the host-inductor. They thus create the possibility of twinning if both parts of the host-inductor act (Fig. 6, *b*). If the graft is placed eccentrically (Fig. 6, *c*), it produces the same kind of results as when placed ventrally. In no case were any triplets formed.

a) *Twins.*—It is an interesting fact that the most perfect twins in all of our series were produced in type 10 (BV/B); the partners are substantially equal in all respects, and each of them possesses an after-feather (Pl. IV, Fig. 20). This result requires the same assumption as in the case of grafts of mid-dorsal origin placed dorsally, that in the halves of the host-inductor the center of induction is displaced toward the equator of the conjoined papilla (Fig. 6, *b*). The presence of after-feathers, which contrasts with the otherwise similar twins produced in the B/BD combination (Pl. I, Fig. 12), indicates a lowering of range of the gradients produced by the centers of induction as compared with the normal. A twin from the heterologous combination SV/B (type 14) is shown in Plate IV, Figure 21, in the third generation (cf. p. 14).

b) *Singles.*—In the case of eccentric location of the graft (Fig. 6, *c*), the result of the dorsal placement of the graft of ventral origin (BV/B, type 10), viz., enlarged after-feather (Pl. V, Fig. 23), is similar to its ventral placement. The amount of material to be controlled is increased, while the range of the gradients remains the same and the material opposite to it is physiologically isolated. The after-feather is formed from host material, and the prospective significance of the graft is completely changed to form part of the vane. The same kind of result is shown in the heterologous combination BV/S (type 16, Pl. VI, Fig. 25). However, in this case, which results in a pseudo-bilateral chimaera, the utilization of the graft (BV) to form one side of the vane is plainly demonstrated.

VI. THE SUPPLEMENTARY EXPERIMENTS

These fall into two classes: (1) grafting experiments (types 17–27) to determine the inducing power of other parts of the papilla than those used in types 1–16, and (2) test of the independent powers of reconstitution of parts used as grafts in order to determine relations to inducing power (types 28–39).

1. THE GRAFTING EXPERIMENTS (TABLE 2, TYPES 17–27)

The results of these experiments will not be considered in detail here. Their

purpose was to determine the distribution and value of inductive power existing in the papilla outside the sectors BD or SD (5–6–5). An example of reduced power of induction of the sector 3–5 (type 20) placed ventrally is shown in Plate I (Fig. 13). The general nature of the results is a diminution of inducing power from the mid-dorsal line to the equator (Fig. 8). Other conclusions to be drawn from these types of experiment will be included elsewhere in the text.

2. THE POWER OF INDEPENDENT RECONSTITUTION OF PARTS (TABLE 2, TYPES 28–39)

A. BD AND SD (TYPES 28, 28*a*, 29, 29*a*)

BD (5–6–5) when isolated by removal of the remainder of the papilla has complete power of reconstitution, producing a feather hardly distinguishable from the normal except that it lacks an after-feather (type 28). When transplanted to an S follicle (type 28*a*), it produces feathers of equal size but with chimaera characters, showing that in the process of reconstitution it has acquired ectoderm cells of S origin; an after-feather was formed in three out of five such cases. The rate of growth of these feathers is the same as the normal (p. 20). The usual absence of the after-feather would indicate that the feather cylinder derived from BD is slightly less in diameter than normal and that the induced gradients in the collar control the entire field at all stages (see p. 24).

SD (type 29) likewise produces approximately normal feathers lacking an after-feather, but both shorter and narrower than usual and with reduced length of fluff. When transplanted to a B follicle, it does not acquire chimaera characters (type 29*a*).

B. BV AND SV (1–0–1, TYPES 34, 35)

These parts offer the greatest possible contrast to BD and SD. They succeed in producing only a few short independent barbs: no rhachis is formed (tuft feathers). Their rate of growth is surprisingly low (p. 21). There is essentially no power of reconstitution in the sense of replacing missing parts, at most only a certain degree of self-differentiation.

When forming part of an intact feather germ, on the other hand, the growth of barbs derived from the same sectors, which begins later than in more dorsal parts of the cylinder, is equal in rate to that of other parts of the cylinder.

Comparison of the foregoing results (Secs. A and B) with the effects of the same sectors used as grafts placed in a mid-ventral position shows that ability to reconstitute runs parallel with power of induction. The sectors possessing the strongest power of induction (BD and SD) have the highest power of reconstitution associated with normal rates of growth, whereas those sectors that lack inductive power (BV and SV) produce only tuft feathers with a much lower rate of growth.

C. PARTS OF INTERMEDIATE ORIGIN

a) *Half-vane feathers.*—In our 1941 paper we described the very characteristic and peculiar (half-vane) feathers derived, in addition to tuft feathers, from ventral halves of B papillae (pp. 116, 132; Pl. V); they are characterized by the presence of only the right or the left side of the vane, and on the other side by "reversed" barbs attached to the rhachis by their apexes and by a variable number of tufted barbs lateral to these. We drew the conclusion that those ventral halves of papillae that produced half-vane feathers included accidentally a small portion of the dorsal half just above the equator which "lacked the power to control the organization of the entire ectoderm, and hence organized and unorganized portions lie side by side."

The present experiments abundantly

confirm this general conclusion, for we have found that only those portions of the inductor that lie close to the equator induce half-vane feathers. Subject to limits of error in technique, we conclude that they are not produced by portions of the papilla ventral to the equator or by the superior portion of the dorsal surface above the position 4 in Figure 3. Table 3 gives the origin of half-vane feathers that have occurred in reconstitution experiments.

Seventy-five half-vane feathers are recorded in these experiments, which included also 40 bilateral feathers more or less defective and 34 tuft feathers. The bilateral feathers must be attributed to dorsal deviations in the operations, and the tuft feathers, which are characteristic productions of isolated portions of the ventral half of the papilla, to ventral deviations in the experiments (cf. Fig. 7). Deviations in the operations cannot be altogether avoided.

If we include only the first six experiments in Table 3, which were definitely intended to resolve the problem of half-vane feathers and their laterality, the situation becomes clearer. Reconstitution tests were first made of equatorial sectors from positions $1\frac{1}{2} - 4\frac{1}{2}$ (Fig. 7, sector *A*) selected from either the right or the left side (*a* and *b*, Fig. 7) of both B and S papillae (types 32-33). Those from the right side produced 4 right-handed half-vane feathers in B and 3 right-handed in S; those from the left side produced 2 left-handed half-vane feathers in B and 2 left-handed in S. Thus the "sidedness" of the part and of the half-vane feathers agreed in all cases. The same experiments produced, in all, 8 bilateral and 5 tuft feathers.

We next tested obliquely cut ventral halves of B papillae (Fig. 7, sectors *A* and *B*): type 38, right-inclined ($1\frac{1}{2}L$–o–$4\frac{1}{2}R$), and type 39, left-inclined ($1\frac{1}{2}R$–o–$4\frac{1}{2}L$). A large number of operations was made, which resulted in seven right-handed and five left-handed half-vane feathers from the right-inclined operations, and in three right-handed half-vane feathers and eight left-handed from the left-inclined operations. The sidedness of part and of product agreed in fifteen cases, but was reversed in eight. There was also quite a large number of bilateral and tuft feathers.

Types 36 and 37 (Table 3) are not inconsistent with the foregoing planned experiments but do not lend themselves to further analysis.

It is demonstrated by all the reconstitution experiments taken together that half-vane feathers are induced only by portions of the inductor that lie slightly above the equator of the papilla, which have been shown to have weak power of induction. But the problem of explaining why the weakest portion of the inductor should induce half-vanes rather than a weak bilateral feather remains. If we were to rely only on the equatorial *quarters* (types 32 and 33), which produce only similar-sided half-vanes, we might arrive at the conclusion that the right and left sides of the inductor are inherently different, though it would be difficult to eliminate the alternative possibility that sidedness of the feathers was due to some differences in the substratum resulting from the operation. The inclined ventral *halves* (types 38 and 39), which differ in composition from the equatorial quarters by the addition of a mid-ventral quarter (Fig. 7), produce reversed sidedness in about one-third of the half-vane feathers. There must, therefore, be some condition not inherent in the inductor, which is the same in both cases, to explain the occurrence of reversal in the inclined halves and not in the equatorial quarters.

If the diagrams (Fig. 7) are regarded

TABLE 3

DERIVATION OF HALF-VANE FEATHERS

The results of types 32 and 33 (Table 2) are here divided into two parts, each according to origin of the reconstituting part from the right (*R*) or left (*L*) side of the papilla (Figs. 7, *a* and *b*). The types below the double horizontal lines (36B [3–0–3] and 37S [3–0–3]) record the reconstitution of ventral halves of papillae in which the side of origin of the half-vane feathers could not be determined.

Experiments		Number Follicles Operated	Half-Vane Feathers		Other Defective Types	
Type	Book No.		Right	Left	Bilateral	Tuft
32*R*..... B($1\frac{1}{2}$–$4\frac{1}{2}$)	703	10	4 (Nos. 10, 13, 14, 17)	0	1	.....
32*L*..... B($1\frac{1}{2}$–$4\frac{1}{2}$)	702	12	0	2 (Nos. 24, 27)	3	.....
33*R*..... S($1\frac{1}{2}$–$4\frac{1}{2}$)	706	19	3 (Nos. 44, 47, 50)	0	2	2
33*L*..... S($1\frac{1}{2}$–$4\frac{1}{2}$)	705	18	0	2 (Nos. 21, 24)	2	3
38, right-inclined.... B($1\frac{1}{2}$*L*–0–$4\frac{1}{2}$*R*)	801	32	7 (Nos. 1, 5, 11, 12, 13, 17, 25)	5 (Nos. 7, 8, 15, 19, 22)	15	2
39, left-inclined .... B($1\frac{1}{2}$*R*–0–$4\frac{1}{2}$*L*)	802	26	3 (Nos. 6, 15, 18)	8 (Nos. 1, 2, 4, 10, 12, 16, 19, 20)	6	4
Total.....	.....	117	17	17	29	11
36B(3–0–3), ventral..	(1941) Several expts	36	10	11	3	10
37S(3–0–3), ventral..	707	25	3 (Nos. 5, 11, 20)	8 (Nos. 1, 2, 3, 4, 7, 8, 9, 15)	2	7
	505*	12	0	3 (Nos. 1, 3, 6)	.....	4
	510*	10	0	3 (Nos. 2, 4, 7)	1	1
	513*	8	2 (Nos. 2, 4)	1 (No. 1)	5	1
Total.....	.....	91	15	26	11	23
Grand total..	.....	208	32	43	40	34

* Half-papillae left over from grafting experiments.

from the position 3, it will be seen that similar-sided half-vanes will arise if formed in a dorsal direction from the rhachis, and reverse-sided if formed in a ventral direction. In some way the addition of B to the sector *A* makes the latter condition possible. The extent of the wounded surface in *A* is equal to that in *A* plus *B* and is thus twice as great proportionally, which leads one to suspect that differences in the healing process rather than merely additional bulk explain the occurrence of reversal in a third

are weaker than normal feathers, i.e., with a more slender rhachis and fewer barbs. The fact that it produces feathers less normal than the sector 5–6–5, though it contains approximately the same amount of inductor material, appears to be connected in some way with its original asymmetry. Half-vane feathers are not produced.

D. RATES OF GROWTH

Individual feathers were selected from various types of the reconstitution ex-

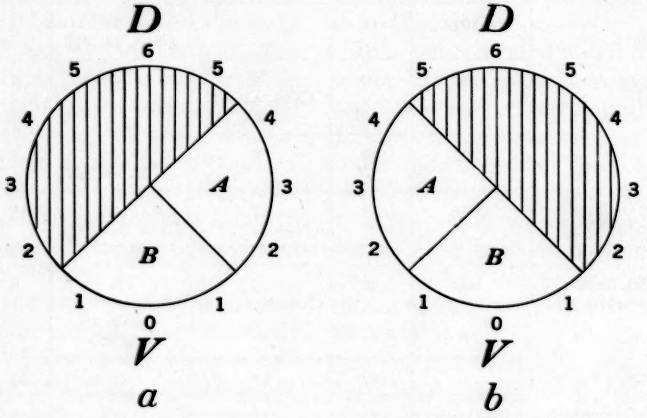

FIG. 7.—Diagram for derivation of half-vane feathers from $1\frac{1}{2}$ to $4\frac{1}{2}$ (segment *A*) and $1\frac{1}{2}$–0–$4\frac{1}{2}$ (*A* and *B*): *a*, right-inclined halves; *b*, left-inclined halves; 0–6 as in Fig. 3. Portion of papilla removed is indicated by vertical bars.

of the derivatives from *A* and *B*. This subject is considered further in Section VIII.

b) *The reconstitution of the sector 3–6.*—To complete the examination of power of reconstitution possessed by parts of the papilla, sector 3–6 was examined (types 30 and 31). This part represents in bulk one-quarter of the entire papilla and possesses one-half of the inductor (cf. Fig. 8). From it there develop bilateral feathers, usually of approximately normal length with asymmetrical vanes, which, unlike those derived from the sector 5–6–5 (BD or SD),

periments and in certain cases were measured at frequent intervals from emergence to completion; in other cases the number of days between plucking and completion of the feather was divided into total length attained; either method is adequate for our purposes. The average growth per day was 1.9 mm. in the case of control B feathers; in the case of BD (5–6–5) it was the same, and in the case of the sector *B* (3–6) also approximately the same. In the case of half-vane feathers derived from B ($1\frac{1}{2}$–$4\frac{1}{2}$) the rate of growth was much less, 1.3 mm. per day. In the case of the ven-

tral sector BV (1–0–1) the growth per day was less than 1 mm. in the first generation. In the case of control S feathers the growth increment per day was 1.59 mm., 1.54 for the sector SD (5–6–5), and 0.88 in the case of the sector 3–0–3.

E. CONCLUSION

The degree of reconstitution of isolated sectors of the papilla is a function of their positions in the whole; the rate of growth of the same sectors corresponds also to the same function. There is a sharp distinction between sectors from the dorsal half of the papilla and those from the ventral half. In the former, which always contain part of the inductor, both degree of reconstitution and rate of growth of sectors run parallel to inducing power. In terms of the quantitative theory of the inductor (p. 22), both degree and rate are functions of quantity of inductor, of which about one-half of the normal amount is adequate for maximum effect. The ventral half of the papilla or the most ventral sector (1–0–1) form tuft feathers devoid of the rhachis. They grow without benefit of inductor, and their rates of growth are below that of any sector possessing part of the inductor; the smaller of these sectors grows much more slowly than the larger.

VII. DEVELOPMENTAL PRINCIPLES

1. INTRODUCTION

The results that have been described may be reduced to a few simple principles of development; they will be discussed under the heads of the inductor and the substratum. We define our use of terms as follows: The term "field"[6] will be used in a purely descriptive sense as defining boundaries in development, whether morphological or physiological. "Induction" is a contact effect that at its maximum causes the "substratum" to realize its full potentialities. Our use of the term "inductor" is not coextensive with any theoretical conception of the process of induction as such but is limited to the inducing portion of the papilla. As we previously inferred (Lillie and Wang, 1941) and as Wang (1943) has clearly demonstrated, the inductor is located in the dermal component of the papilla. In the development of the feather the "substratum" is represented in general by the epidermis of the papilla, but in particular by its principal derivative, the collar. The term "gradient" is limited to the collar; it defines a linear order of action and implies a high point at one end (the "dominant region") and a low point at the other. The physiological effects of the gradient have a certain "range," measured from the dominant region, which diminishes somewhat with age. Parts of the collar within the range are not capable of independent development. Any part of the collar that lies outside the range is "physiologically isolated," to use Child's apt expression, and is capable of independent development.

[6] See Weiss (1939) for a discussion on the use of this term.

2. THE INDUCTOR

We have shown that the inductor is located in the dorsal half of the papilla and that its inducing power is bilaterally distributed from a maximum at the center to a minimum near the equator of the papilla. It possesses no axial differentials,[7] but these are independent properties of the substratum. Exact determination of the ventral limit of the inductor is hardly possible because of the difficulty of distinguishing between the

[7] We find that the central portion of the inductor (BD), placed ventrally with reversed axis, may induce a normal twin; but the experiment is unusually difficult for mechanical reasons, and we have only one good example. Our conclusion rests mainly on the negative evidence.

effects of minimum inducing power and the independent power of development of physiologically isolated material in the collar. However, it is possible that the minimum expression of actual induction is the formation of half-vane feathers (p. 18).[8]

The power of reconstitution of isolated sectors of the papilla is proportional to

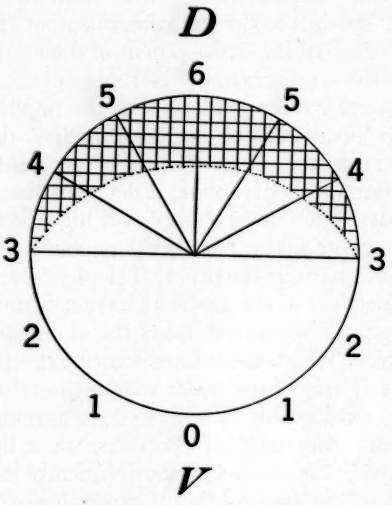

FIG. 8.—The quantitative theory of the inductor. The equal squares are distributed in correspondence with the distribution of inductive power as shown by the experiments. This produces the lunate form. 0–6 as in Fig. 3. *D*, dorsal; *V*, ventral.

the inducing power. The sector of highest inducing power (BD or SD, 5–6–5) is capable of producing a feather of normal size and form, though usually lacking an after-feather. On the other hand, a sector of the same size with no inducing power (e.g., BV or SV, 1–0–1) produces a dwarf lacking a rhachis or any bilateral organization—a mere tuft of isolated barbs. Sectors of intermediate origin that include the level of the equator (types 32 and 33) typically produce short half-vane feathers. Above this to position 5 defective bilateral feathers are produced. Inducing power is parallel not only to the power of reconstitution of corresponding isolated sectors but also to the rate of growth of such sectors (p. 20). We thus come to the conclusion that induction in the feather germ consists in acceleration of development in the substratum.

These properties lead to a quantitative interpretation of the inductor. It consists of a certain quantity of material distributed in cross-section in the form of a crescent in the derma of the papilla next to the epidermis (Fig. 8). Inducing power bears a proportional relation to quantity of inductor: the amount contained in the sector 5–6–5 is sufficient for maximum effect on the substratum; lesser amounts are increasingly inadequate. This distribution of inductor material explains also the distribution of power of reconstitution and the rates of growth of the various sectors of the papilla. The very striking fact (Tables 1 and 2, last column) that the modified forms of feathers, whether produced by addition of inductor material (grafting) or by its reduction (reconstitution of parts), are repeated in successive generations leads to the inescapable conclusion that quantity of inductor, once established experimentally, is not capable of regulation in the stages of the papilla with which we deal.

Induction appears to depend on contact of inductor and substratum. Therefore, in normal development the effect of acceleration, which is distributed over the entire dorsal half of the epidermis of the papilla, is graded from the center out on each side in proportion to quan-

[8] In the amphibian embryo the inducing capacity of the inductor of the neural plate decreases laterally from the center. Lateral halves of the inductor induce symmetrical neural plates, but smaller lateral portions may induce asymmetrical plates, especially in later stages of the gastrula. These data bear undeniable resemblance to the inductor of the feather (cf. C. M. Child, 1941, p. 459, and references there).

tity of inductor. The dorsal field of parallel barbs (Lillie and Wang, 1941) is the immediate result of this induction. The rhachis arises a little later in the mid-dorsal, or dominant, region. On this conception the form of the inductor is significant for the origin of the gradients in the substratum. Thereafter, the gradients extend independently to an extent determined by the value of the dominant region which is dependent on quantity of inductor reorganize to the form of a crescent on each side (Fig. 9, *c*). In the process of induction which follows, the dominant regions of the collar are situated opposite to one another, and the rhachi of the twins arise in this position, which is about equidistant between the center of the graft and the ventral locus (o) of the host. Complete and equal twins result when grafts of ventral origin are used (Pl. IV, Fig. 20). Displacement of

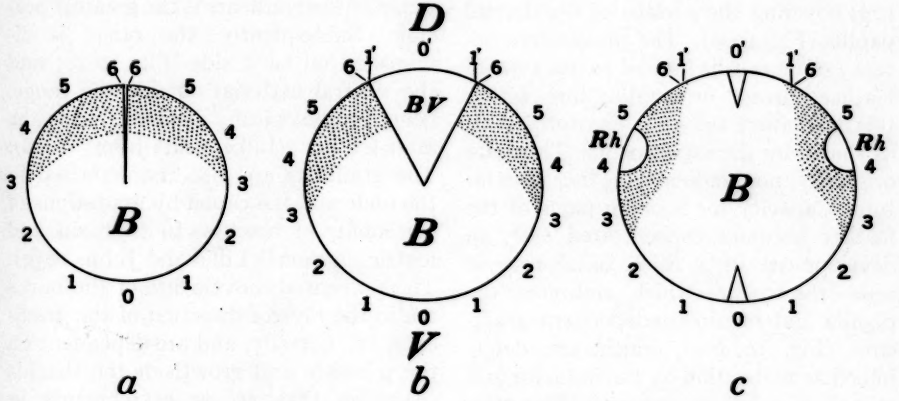

FIG. 9.—Diagrams illustrating reorganization of lateral halves of the inductor (*stippled*). *a*, Division of the inductor; *b*, insertion of the sector BV (1′–o′–1′); *c*, reorganization of the lateral halves of the inductor and location of rhachi and triangles. This illustrates the phenomenon of displacement of centers of induction (text, p. 16). o–6 as in Fig. 3.

inductor. Although loss of quantity of inductor cannot be replaced, parts reorganize, resume the original crescentic form, and establish gradients in the substratum on the same principle as the intact inductor, though with reduced range (Fig. 9).

The question of displacement of the center of induction referred to in connection with twins from dorsally placed grafts (pp. 13 and 16) may now be understood. In these cases (Fig. 9) the insertion of the graft is preceded by operative division of the inductor into its right and left halves. The graft is then inserted (Fig. 9, *b*), and the halves of the centers of induction is thus to be interpreted as due to rearrangement of inductor material on each side from half-crescents to whole crescents of half-size. It will be observed (Fig. 9) that the rhachi are lateral in position, according to this interpretation, instead of dorsal and ventral, respectively, as in the B/BD combinations (type 1). An interesting confirmatory feature not noted previously is that in the living bird the twin-feathers (type 10) are placed on edge with reference to the body of the bird, i.e., the surfaces of both partners are rotated 90° from the normal.

We have not been able so far to identi-

fy the inductor by histological differentiation within the substance of the papilla. The form that we have given it is deduced from the data of the experiments and constitutes a consistent summary of the results. Further study by different methods will be necessary to determine the physical basis of its properties.

3. THE SUBSTRATUM

The substratum is represented originally by the thin single layer of epidermal cells covering the surface of the dermal papilla (Fig. 10, *a*). The prospective potency of its cells is limited to one type of feather—breast or saddle; but within this limitation the cells are totipotent, as shown by the experiments. There are originally no gradients in the substratum. Capacity for forming parts of the feather becomes concentrated early in development in a thick basal ring of cells—the collar—which embraces the papilla and requires independent gradients (Fig. 10, *b–e*), which are determined as to location by the inductor and as to range by its quantity. The relations of the feather cylinder to the collar and the papilla shown in Figure 11 (from Lillie, 1940) are constant throughout the entire period of regeneration.

A. THE GRADIENTS IN THE COLLAR

a) *In normal development.*—The ventral triangle forms approximately opposite to the rhachis, i.e., in a ventral position in the feather cylinder (Fig. 10, *b*). It is composed of a tongue of rapidly multiplying epidermal cells which produce barb apexes on each side continuously. These then grow independently and move toward the rhachis in the tangential stream. The features of the ventral triangle that demand attention are, first, its position as determined by the gradients and, second, the rapid multiplication of its cells that have retained the capacity to form complete barbs, originally inherent in all parts of the epidermis of the papilla; all undetermined material thus comes to be located in the ventral triangle.

The gradients in the collar are marked morphologically by lengths of barbs decreasing from the greatest at the rhachis dorsally to the least at the ventral limit. In the course of normal development the right and left gradients meet at the ventral triangle (Fig. 10, *b*). At this time the range of the gradients is the greatest possible. Subsequently, the range is diminished on each side (Fig. 10, *c*); and the ventral material outside the range, being physiologically isolated, forms the after-feather (Lillie and Juhn, 1938). The gradients are also characterized in the male and the capon by gradations of thresholds of reaction to thyroxin and female harmone (Lillie and Juhn, 1932). The tangential movements of the barbs are in the reverse direction of the gradients, i.e., dorsally, and are dependent on the presence and growth of the rhachis to which they secure attachments in serial order by the barb petioles (Lillie and Wang, 1941). These are conditions, among others, determining the pattern of the feather.

The regenerative capacity of the papilla is always ready to be exercised when the feather is plucked. We do not know whether or not the inductor continues to sustain the gradients in the collar during development of the feather after the first induction. In our fifth study (Lillie and Wang, 1941), relying on some experiments of Woitkewitsch (1936), we adopted the second alternative; but we no longer believe that his experiments justify the conclusion that we drew from them. The question is immaterial so far as the present experiments are concerned, for relations of the dermal papilla and the collar (Fig. 11),

however modified by the experiments, are not altered during development.

b) *Experimental.* (i) *General.*—That the gradients in the collar are determined by the inductor is proved by the grafting of a supplementary inductor (Table 1, types 1–8); gradients may thus be caused to appear in any position in the collar, and two or even three sets may be produced simultaneously (twins and triplets). Independent feathers then form with reference to the double or triple centers of organization. Rhachi and triangles may therefore appear in any position, though always in reciprocal relations to one another; and in consequence the positions of barb levels, in comparison with the normal, are shown to be interchangeable. These conclusions follow from the experiments described in Sections V and VI.

When two strong centers of induction (host and graft) are simultaneously present, the induced gradients in the collar extend from each center until they meet (Fig. 10, *d*), and the two places of meeting are invariably marked by triangles, where new barbs are produced and proceed to move tangentially toward the two rhachi. The two pairs of gradients are thus in competition for control of the substratum. When the

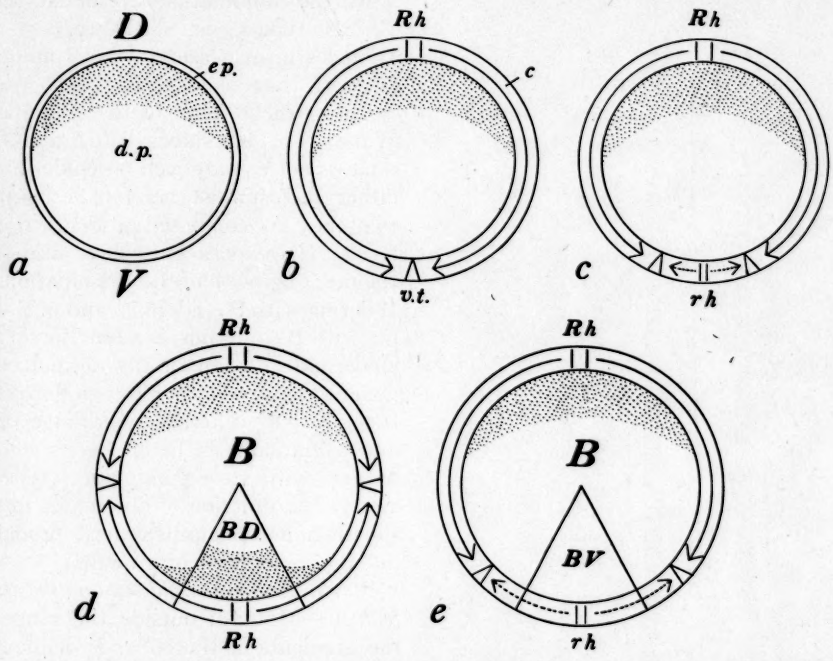

FIG. 10.—Theory of the gradients in the collar and their range shown in cross-section. *a*, The papilla; *b* and *c*, two stages in normal development; *d*, the gradients in type 1, Table 1 (B/BD); *e*, the gradients in type 9 (B/BV). The thin layer of epidermis of the undeveloped papilla, *a*, forms the thick epidermal collar in the other diagrams. The diameters are increased in *d* and *e* by the amount of the graft. The direction and range of gradients in the collar are represented by the concentric arrows, broken in the case of the after-feather (Figs. *c* and *e*). The stippled area is the inductor; in *d* it is shown for the graft BD before and after reorganization. *c* = collar; *d.p.* = derma of the papilla; *ep.* = epidermis; *Rh* = rhachis of the main feather and of the induced feather also (in *d*); *rh* = rhachis of after-feather; *v.t.* = ventral triangle.

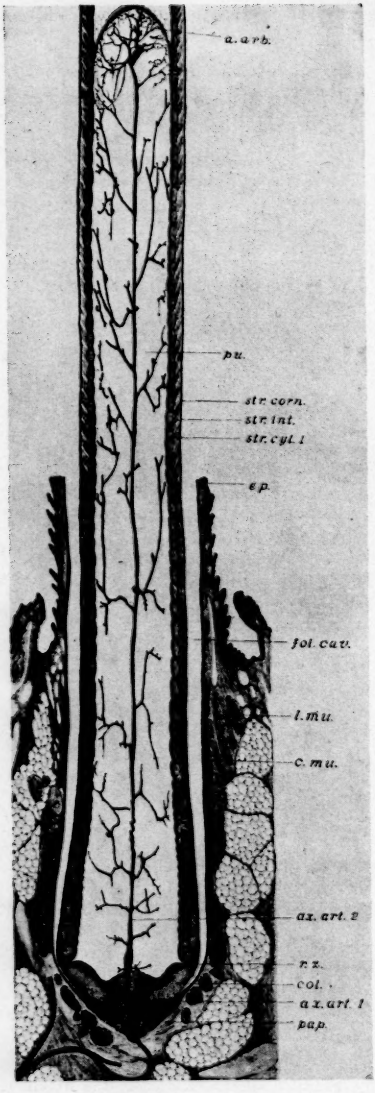

FIG. 11.—Longitudinal section of the feather cylinder and follicle on the twenty-first day of regeneration; for special reference to the relations of the collar and papilla. After Lillie, 1940. *a. arb.* = apical arborization; *ax. art. 1* = axial artery in the papilla; *ax. art. 2* = axial artery in the pulp; *c.mu.* = circular muscles of the wall of the follicle; *col.* = collar; *ep.* = epidermis; *fol. cav.* = cavity of follicle; *l.mu.* = levator muscle of the feather; *pap.* = papilla; *pu.* = pulp; *r.z.* = ramogenous zone; *str. corn.* = stratum corneum (forms sheath); *str. cyl. 1* = stratum cylindricum: the part in contact with the pulp destined to form the pulp membrane and the barb membrane; *str. int.* = stratum intermedium (forms feather).

central portion of the inductor (BD or SD) is placed ventrally in homologous combinations (types 1 and 3), the collar gradients are in opposite directions and of equal range, so that each controls half of the substratum; triangles form halfway between them (Fig. 10, *d*). But when the combinations are heterologous (B/SD, type 5; or S/BD, type 7), the triangles form nearer to the S inductor (Fig. 4), thus demonstrating the greater range of the B than of the S gradient. Wang (1943) has shown that B and S inductors act equally well on epidermis of either tract; it must therefore be assumed that they are composed of identical material. His experiments show also that the rate of growth of the combinations of B derma with S epidermis, and of S derma with B epidermis, is a function of the epidermal and not of the dermal component. It would therefore follow that the apparent differences of range of B and S gradients in heterologous combinations with strong inductors (types 5 and 7) is a function of differences in the substratum (epidermis), most probably differences in rates of growth.

ii) *Physiological isolation and the after-feather.*—Material outside the range of the gradients of the collar is defined as physiologically isolated. Any development in such material is therefore also without benefit of the inductor and hence may be termed "autonomous." In normal development as part of the collar it is capable of a high degree of organization and forms the small, independent after-feather with its own rhachis and bilateral organization. This is correlated with, and presumably dependent on, the fact that as part of the

collar it shares in the uniform, rapid rate of growth that characterizes the collar throughout its whole extent. When the corresponding part of the papilla is physically isolated, its rate of growth is much slower, and it forms only a tuft of barbs without rhachis or bilateral organization (types 34 and 35).

The amount of material physiologically isolated is determined by the range of gradients induced in the collar, which can be modified experimentally. The variables established are: first, the intensity of action of the complete or partial inductors concerned, with corresponding variations in range of the gradients of the collar; second, the extent of the field of the collar in which the gradients operate, which may be increased by grafts or diminished by operative removal of parts of the papilla.

A *graft of dorsal origin* (BD or SD, 5–6–5) placed ventrally establishes a competing inductor which, though less in amount, is equal in action to the inductor of the host; and it is obvious that each set of gradients induced in the collar must operate within a much smaller field than normal, in spite of the slight increase in circumference of the collar due to the graft (Fig. 10, *d*). Hence no physiologically isolated material should occur during development, and no after-feather should be formed. If the two sets are not opposite to each other, the material within the field of one is diminished and that of the other increased relative to one another, and so physiologically isolated material may occur in the case of the latter. To this corresponds the fact that no after-feathers occur in the majority of B/BD and S/SD combinations and, when present, only one partner is provided with one (Table 1, types 1 and 3). In type 7 (S/BD) ten pairs of twins were produced, all without after-feathers except one, which possessed a single one. Similarly, although the sectors BD and SD (5–6–5) when isolated produce quite normal feathers (types 28 and 29), the after-feather is lacking; this is due presumably to diminution of the field within which the gradients of the collar operate, to such an extent that no physiologically isolated material remains.

Grafts of ventral origin (BV or SV, 1–0–1) placed ventrally (Table 1, types 9, 11, 13, 15) produce no change in the original inductor system, but, in contrast to grafts of dorsal origin, the field within which the gradients of the collar operate is increased (Fig. 10, *e*); and this is true whether the graft is placed ventrally or in an eccentric position (Fig. 6). The amount of the physiologically isolated portion of the collar is therefore increased, seeing that the gradients remain the same. The result is to increase the size of the single after-feather or to produce more than one (Pls. V and VII).

Increase of size of the after-feather is accompanied by increase in length, and thus earlier time of origin, as compared with the normal after-feather. This may be so considerable, if only one after-feather is formed, that it overlaps the vane of the main feather (Pl. V), and some of the barbs of the enlarged after-feather then possess vanelike tips, which in heterologous combinations may possess characters of the graft. Multiple after-feathers do not overlap the vane; it follows that they result from later activation than in the case of the single enlarged after-feather. The maximum effect, actually five distinct after-feathers, was produced in type 13*a*, in which the amount of added ventral material was tripled, 3–0–3 as against 1–0–1 (Pl. VII). Those cases (Pl. V, Fig. 23) in which the graft was placed eccentrically (Fig. 6, *c*) prove that the physiological isolation is not due to location of the graft, which does not itself enter into formation of the after-

feather in this case. Limitation of range of the collar gradients is the explanation in the one case, as well as in the other.

The single enlarged after-feather has a single center of organization like the normal after-feather; multiple after-feathers, which arise from the same amount of physiologically isolated material, have multiple centers. The former arises at an earlier stage of development than the latter, as shown by their greater length. But we cannot explain why activation is earlier in different cases. It seems obvious that an organizing center is stronger when it arises earlier than when it arises later; at least it controls all the physiologically isolated material, whereas the later centers control only part, leaving residues for subsequent organization.

It is possible to eliminate the chance of weak inductive action of the grafts of ventral origin even in the formation of an extremely large after-feather: when the graft of ventral origin is placed eccentrically in the dorsal half of the papilla far from the site of origin of the after-feather, it forms part of the vane of the single feather, and the enlarged after-feather arises from ventral material of the host (pp. 15–16).

The reconstitution experiments furnish an additional test of the conception that after-feathers arise from physiologically isolated parts of the collar. In these experiments the papilla is reduced instead of being increased. Depending on the amount of regeneration of the papilla (p. 17), the circumference of the collar is correspondingly reduced. Strong inductors possessed by a reconstituting part should therefore induce gradients in the collar that would control the entire field throughout regeneration, leaving no physiologically isolated material to form an after-feather. The types of experiments concerned are 28, 28*a*, 29, 29*a*, 30, and 31 (Table 2); with the exception of 28*a*, none of these produced after-feathers. In the exceptional case the part BD (5–6–5) was transplanted to an S follicle, and so the experiment was complicated by unknown factors. Other experiments involving lower levels of the inductor (types 32, 33, 37, 38, and 39) produce half-vane feathers typically, and the majority of these possess after-feathers, though some do not; but the range of gradients with reference to extent of field is quite unknown in these cases. The reconstitution experiments taken together strongly support the conception of physiological isolation.

iii) *Half-vane feathers.*—The data are presented and discussed on pages 17–20. Their interpretation in terms of the quantitative theory of the inductor requires the assumption that in the reorganization of small lateral portions of the inductor a half-crescent is formed instead of a whole crescent.[9] On the theory of induction of gradients in the substratum which we have presented, a half-crescent would induce a unilateral gradient in the substratum with the rhachis arising at its dominant region; thus a feather would be formed with half of a vane on one side and tufts of barbs on the other. This presents a formal theory of half-vane feathers in agreement with the general theory of the inductor.

If the half-vanes derived from right and left sides, respectively, of the inductor always differed from the side of origin—right half-vanes from the left side and left half-vanes from the right side—we could then suppose that the small lateral margins of the inductor that

[9] However simple the inductor may appear to be, nevertheless its reorganization implies an intrinsic pattern in its substance. The formation of only half of that pattern in small portions bears a general resemblance to the regeneration of those short pieces of tubularian hydroids or of planarians in which only part of the pattern (apical region) is formed (cf. C. M. Child, 1941, pp. 332–33 and 365).

induce them did not reorganize but retained their original form (p. 23). However, the reverse is usually the case (Table 3); hence the necessity for assuming reorganization of the inductor substance into half-crescents. In the reconstitution of quarters from the equatorial region ($1\frac{1}{2}$–$4\frac{1}{2}$) same-sided half-vanes are formed; the point of the half-crescent is oriented dorsally (p. 18). In oblique halves ($1\frac{1}{2}$–o–$4\frac{1}{2}$) it may also be oriented dorsally, but in a minority of cases the reverse happens, producing opposite-sided half-vanes. This suggests that quantity of the substratum, or of the derma, of the papilla may affect the reorganization of the inductor (p. 23). Until more is known about the nature of the inductor, it does not seem possible to analyze this problem further.

VIII. SUMMARY

The mechanism of development of the feather was investigated by various new types of experiments, including grafting of selected parts of the papilla (the feather-germ) to host-papillae and study of the independent power of development of such parts. A graft derived from the dorsal half of the papilla inserted in the center of the ventral surface of host-papillae induces a separate feather, twinned face-to-face with that of the host. The central third of the circumference of the dorsal half induces a twin feather equal in all respects to that of the host; power of induction of parts of the papilla decreases from this sector to the equator of the papilla, where it ceases. Similar grafts derived from the ventral half of the papilla have no inducing power but produce enlargement of the after-feather. The independent power of development of the parts used as grafts, when isolated, and the rates of growth of such parts run roughly parallel to inducing power. Half-vanes are produced from sectors of the papilla containing only a small part of the periphery of the dorsal half of the papilla immediately above the equator.

Twinned feathers may also be produced by division of the dorsal half of the papilla as far as the center and by insertion of a graft to prevent healing of the cut. If the graft is of ventral origin, similar and equal twins may be produced; if of dorsal origin, triplets are formed in some cases.

Inducing power is attributed to an inductor located in a dorsal position in the derma of the papilla, decreasing in amount from the mid-dorsal line to the equator. Its effect is regarded as acceleration of developmental processes in the ectoderm (substratum) and the production of gradients of action of limited range in the collar. Material beyond the range is physiologically isolated in this sense and, by virtue of autonomous power of development, produces one or more after-feathers varying in size in proportion to the amount of physiologically isolated material.

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PLATES I–VIII

Photographs of illustrative examples starred in Tables 1 and 2. Partners in twins and after-feathers displaced for purposes of illustration. *D* = dorsal surface; *V* = ventral surface.

PLATE I

FIG. 12.—Type 1, Table 1, B/BD; 403:10 (first generation). The graft-induced partner (*right*) is distinguished only by its minor defects from the host-partner and by the fact that before plucking the latter lay over the former. No after-feather. Natural size. (See text, p. 12.)

FIG. 13.—Type 20, Table 2, B/B(3–5); 603:2 (first generation). The graft-induced partner (*right*) is much shorter than the host-induced partner and also defective. No after-feather. The sector 3–5 has much less inducing power than the mid-dorsal sector 5–6–5. Natural size. (See text, p. 17.)

PLATE II

FIG. 14.—Type 3, Table 1, S/SD; 404:10 (second generation). The graft-induced partner (*right*) is narrower but otherwise equal to the host-partner. (See text, p. 12.) No after-feather. ×4/5.

FIG. 15.—Type 5, Table 1, B/SD; 407:4 (second generation). The graft-induced partner (*left*), a transverse chimaera with S apex and B base, is equal in length to the host-partner. No after-feather. (See text, p. 12.) ×4/5.

FIG. 16.—Type 7, Table 1, S/BD; 408:10 (first generation). The graft-induced partner (*right*) is a longitudinal chimaera with B apex and center and S margins characteristic of longitudinal chimaerae. No after-feather. (See text, p. 12.) ×4/5.

PLATE III

FIG. 17.—Type 2, Table 1, BD/B; 412:8, triplet (first generation). The central graft-induced member has only one half-vane, showing that it lost out in competition for control of the substratum to the host-member on the left, with which its rhachis soon unites. No after-feather. (See text, p. 14.) Dorsal view. Natural size.

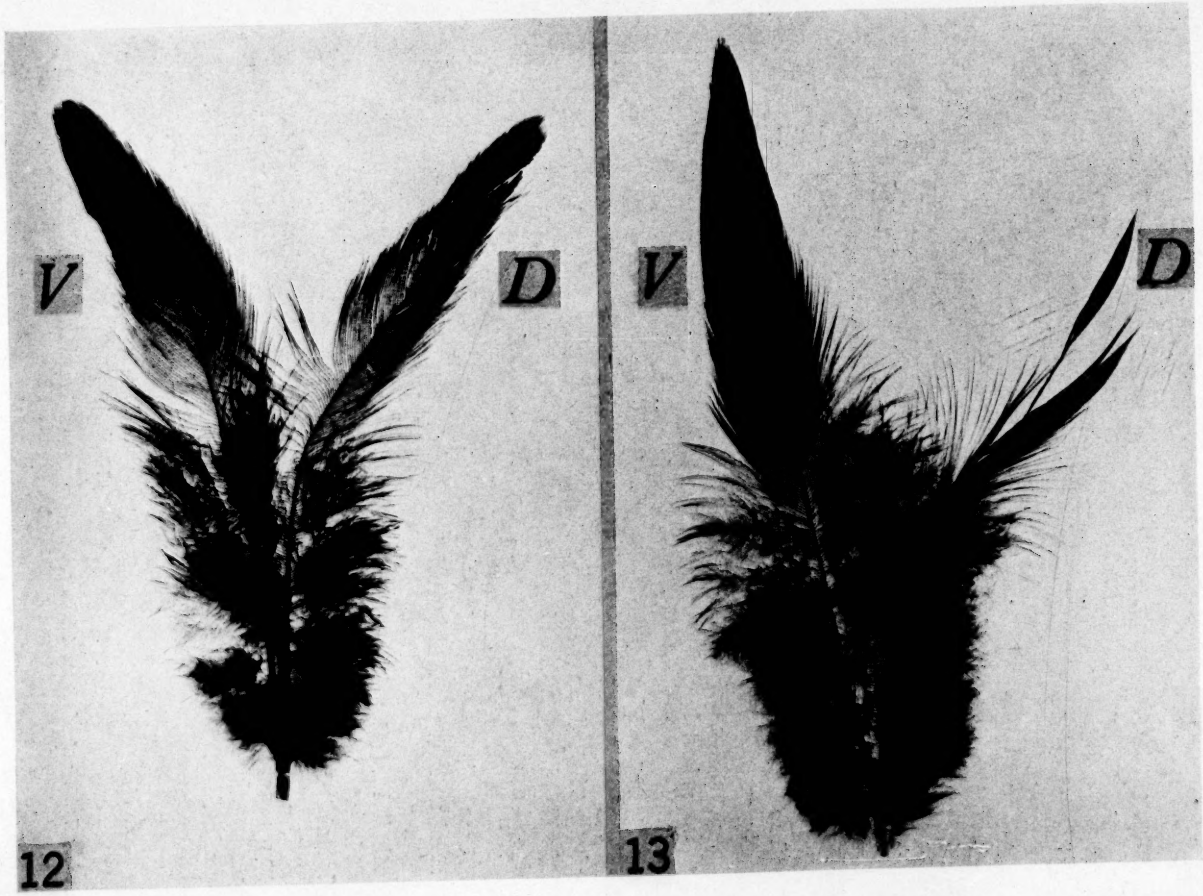
FIG. 18.—Type 2, Table 1, BD/B; 412:6 (first generation); conjoined twins. In this case the graft failed to divide the inductor of the host; partners arise independently from closely situated host- and donor-inductors. Dorsal view. One after-feather. (Cf. Fig. 6, *b*.) Natural size.

FIG. 19.—Type 6, Table 1, SD/B; 401:5 (first generation); triplets. The central, graft-induced member (pure S) has only one half-vane (cf. Fig. 17). Dorsal view. No after-feather. (See text, p. 14.) Natural size.

PLATE IV

FIG. 20.—Type 10, Table 1, BV/B; 405:9 (second generation). This twin is the result of activation of both halves of the host-inductor and utilization of the graft by both partners. Each partner has an after-feather. (Cf. Fig. 7, *b*.) Natural size.

FIG. 21.—Type 14, Table 1, SV/B; 401:10 (third generation). As in type 10 (Fig. 20), the two partners are products of the halves of the split host-inductor. The graft (SV) is


V
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12
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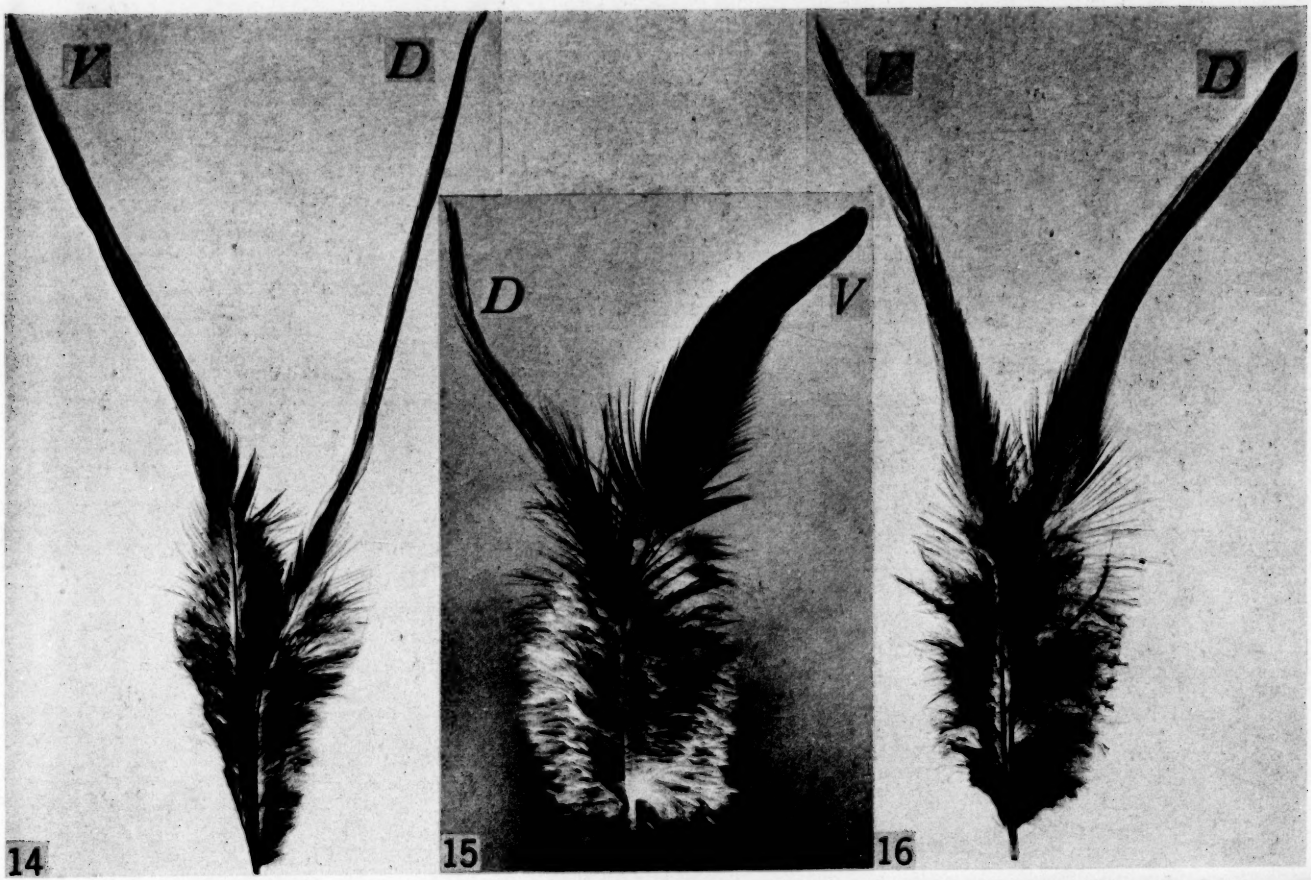
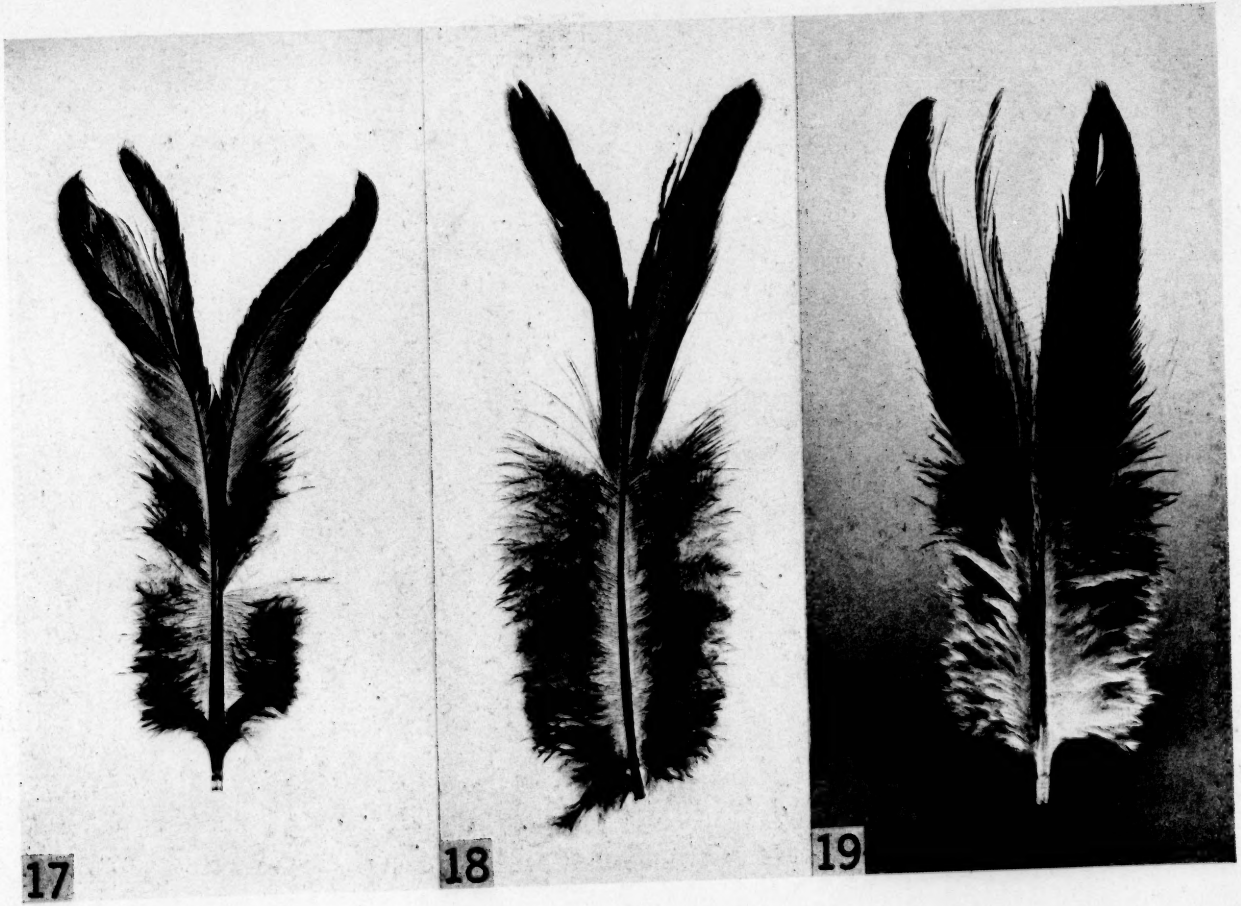
D
13

PLATE II

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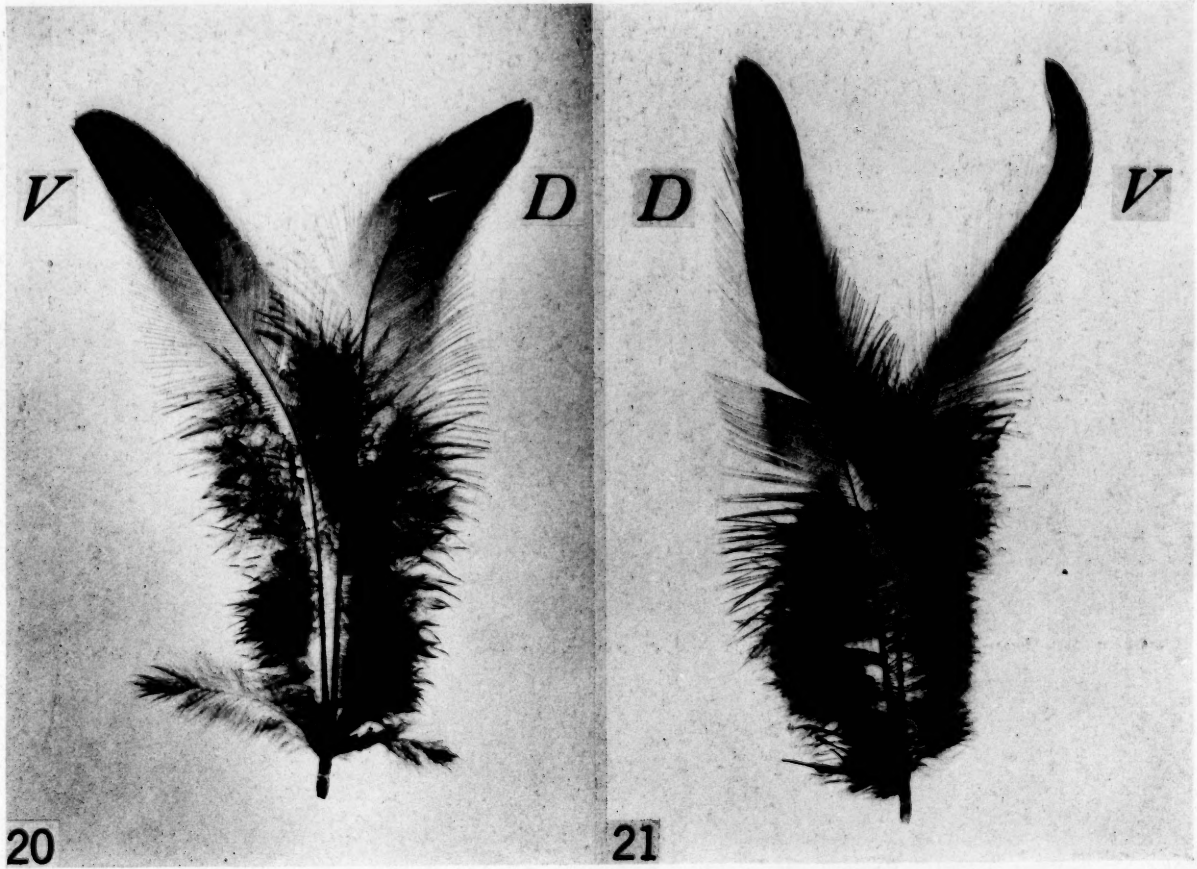
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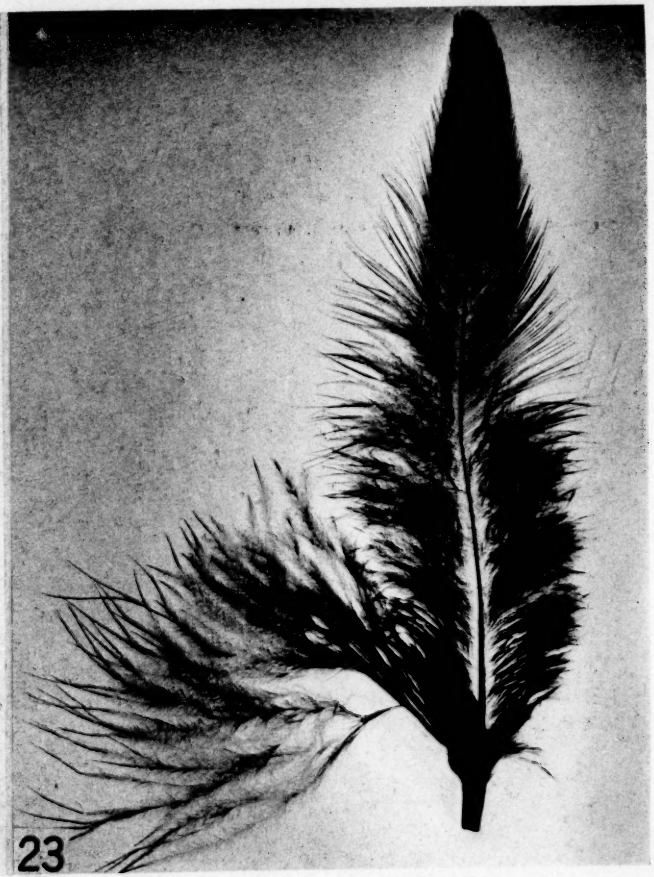
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PLATE VI

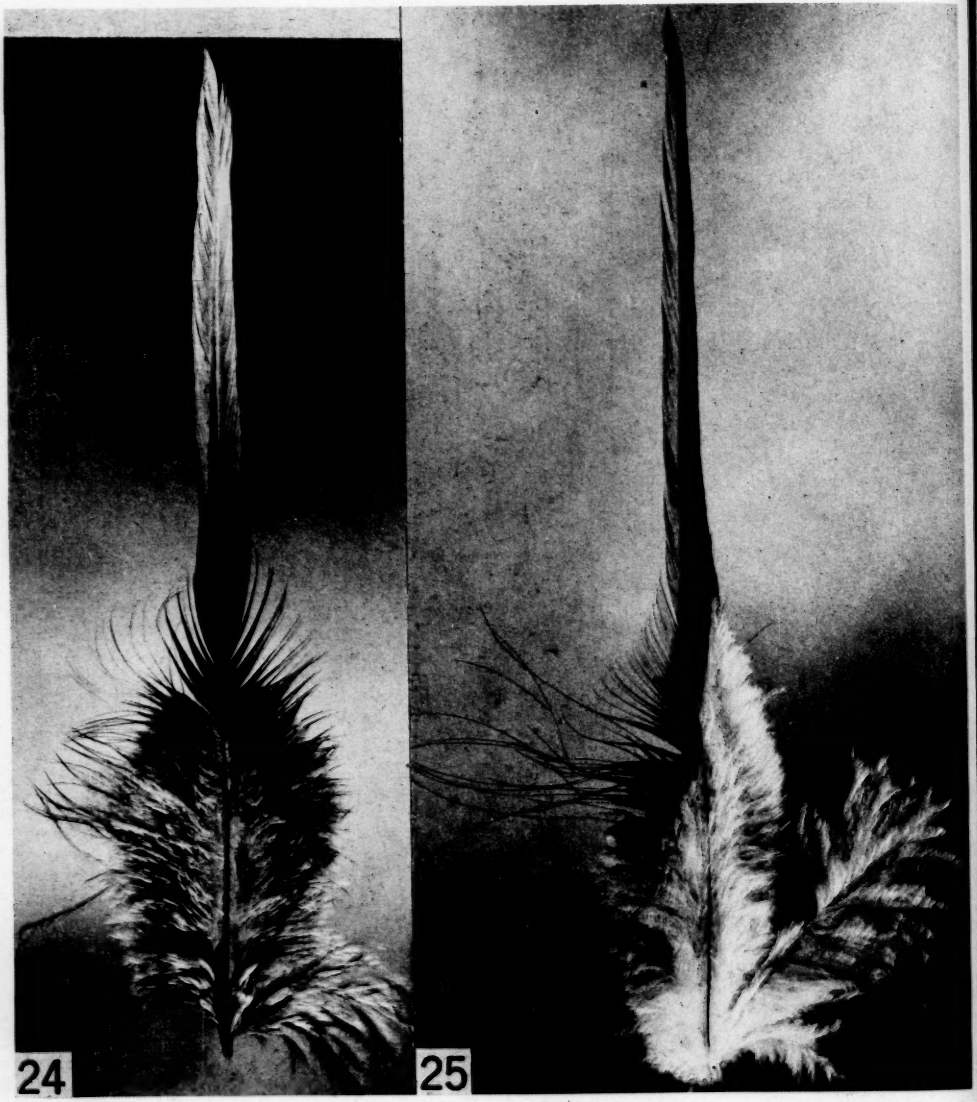

PLATE VII

PLATE VIII

utilized to form part of the left side of one partner and part of the right side of the other (seen from opposite surfaces in the figure), as shown by lacy and S-pigmented margins. No after-feather. (See text, p. 16.) Natural size.

PLATE V

FIG. 22.—Type 9, Table 1, B/BV; 412:1 (first generation). An extraordinarily enlarged after-feather has resulted from the ventrally inserted graft of ventral origin. (See text, p. 15.) Dorsal view. Natural size.

FIG. 23.—Type 10, Table 1, BV/B; 405:6 (first generation). In this case the graft was presumably located eccentrically to the left of the host-inductor (cf. Fig. 7, *c*). The huge after-feather represents physiologically isolated ventral material of the host. (See text, p. 16.) Dorsal view. Natural size.

PLATE VI

FIG. 24.—Type 11, Table 1, S/SV; 413:1 (first generation). In this combination, enlargement of the after-feather occurs for the same reason as in type 9 (cf. Fig. 22), but to a much less extent. (See text, p. 16.) Dorsal view. Natural size.

FIG. 25.—Type 16, Table 1, BV/S; 402:8 (first generation). In this case the graft was located eccentrically beside the host-inductor (cf. Fig. 7, *c*) and was utilized in forming part of the right vane, resulting in a pseudo-bilateral chimaera. The excess of physiologically isolated ventral material caused the enlargement of the after-feather (cf. Fig. 23). Dorsal view. Natural size.

PLATE VII

FIG. 26.—Type 13*a*, B/S(3–0–3); 407*a*:8 (first generation). The large amount of physiologically isolated ventral material introduced by the graft formed five distinct after-feathers. (See text, p. 16.) Dorsal view. Natural size.

PLATE VIII

FIG. 27.—Type 1, B/BD; 403:14 (third generation) at extreme left, and three normal B feathers as controls as they appeared on the thirtieth day of regeneration *in situ* on the bird. (See text, p. 4.) The grafted specimen produced complete and equal twins, seen emerging above the sheath. Note the difference in the diameter of the grafted and the control cylinders. Measurement in the photograph at the mouth of follicle shows 9.0 mm. for the experimental, as against 7.3 mm. for average of the controls. Dorsal view. ×3.5.

THE FAT CONTENT OF PAGURUS PARASITIZED BY PELTOGASTER AND ITS RELATION TO THEORIES OF SACCULINIZATION

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THE effects produced by parasitic crustaceans, primarily the Rhizocephala and Epicaridea, on their decapod hosts have been the subject of numerous investigations since the problem was first treated by Giard (1886). In the main, these have been morphological studies centered about the phenomenon of parasitic castration and concomitant external modifications (see Hanström, 1939, for a fairly comprehensive bibliography). General physiological effects have received relatively little attention.

That sacculinization brings about a disturbed fat metabolism in the crabs *Carcinus* and *Inachus* infested by *Sacculina neglecta* (now *Drepanorchis neglecta*) was shown by Smith (1911, 1913) and Robson (1911). These workers considered the blood of parasitized crabs to be richer in fat than that of normal animals and proved that more fat was de-

[1] The authors wish to acknowledge the great assistance rendered by Sister Clarita Marie Young, O.P., who, under our direction, performed the laboratory work for the morphological portion of this investigation.

posited in the liver of infested crabs. This was interpreted as meaning that the *Sacculina*, by continually abstracting fatty material from the blood of the host, stimulated its constant production in excess. Smith regarded this fat as yolk material, similar to that which is stored in the ovary of a normal female crab at maturity. Its presence in excess in parasitized males would account, he believed, for their assumption of female characters. Hughes (1940) studied *Upogebia* parasitized by the epicaridean *Gyge branchialis* and likewise found an increase in fat content in parasitized males. He considered his results as essentially in agreement with the views of Smith.

Increased production of fat in the liver is not necessarily the rule in such cases of parasitization, as is evidenced by the incidental remark of Pierre (1935) that the liver of one specimen of *Diogenes pugilator* parasitized by *Septosaccus cuenoti* was poorer in fat than that of normal animals. Since her concern was with the liver of normal Paguridae, she did not pursue the observation further. It is the purpose of the present paper to report the results of studies on the fat relationships in the hermit crab, *Pagurus pubescens* Kröyer, parasitized by *Peltogaster paguri* Rathke—studies that show a marked impoverishment of fat in the host liver as a result of infestation by a rhizocephalan—and to point out their bearing on current theories of sacculinization.

MATERIAL AND METHODS

Infested and normal hermit crabs were collected in Frenchman's Bay, Maine, and preserved in formalin. Only mature animals were used for this study, and these were secured solely during the months of July and August. Females of *P. pubescens* are not yet ovigerous at this time of year, but the ovaries are already full and the eggs large.

Morphological and chemical methods were employed to determine the fat relationships. Both procedures have their advantages and disadvantages. The former allow an exact study of the localization of fat and permit estimation of the relative amounts of fat demonstrable, once norms have been established for comparing the stained sections. They fail, however, to yield truly quantitative results. No single stain, or the use of different fat stains, will demonstrate all the fatty material that is actually present and that can be extracted from an organ or organism by chemical methods. Chemical methods, on the other hand, give a true picture of the total fatty substances present, but their usefulness in studying the distribution of fat in various organs will depend upon the difficulties experienced in isolating the organ in question from its surroundings. In general, they will be quite useless for determining the fat content of single tissues or cells.

For the morphological fat studies, five classes of material were used: normal males, parasitized males, normal females, parasitized females, and the external sacs of the parasites themselves. The fat distribution in the crab was confined to a study of the liver. In the case of parasitized animals this allowed a simultaneous study of the fat present in the roots of the parasite, since these structures are closely intermingled with the liver tubules. Separate slides were made of the external sacs of *Peltogaster*, which were selected to cover a range in size from 2.5 to 14 mm.

The specimens were imbedded in gelatin according to the method of Gaskell-Gräff (Romeis, 1932) and sectioned on a freezing microtome. Sections were cut 12 μ thick in the case of the liver and roots and 18 μ thick in the case of the external parasite. Staining was per-

formed with Sudan III, Scharlach R, or Sudan IV; or the presence of fat was demonstrated by osmic acid, using Krajian's (1940) procedure for frozen sections. All these methods yielded identical results with respect to amount and distribution of fat. The stained sections were mounted in glycerin jelly or glychrogel.

For the chemical fat studies, normal and parasitized male and female hermit crabs were used in their entirety, save that the external sacs were removed from the parasitized specimens. These sacs were subjected to separate fat determinations. The method of fat determination employed by us is a modification of the one introduced by Kumagava and Suto (1908). The specimens were first washed with distilled water and then dried at 105° C. for about 18 hours. After weighing, they were heated 2 hours on a boiling water-bath with 15 per cent NaOH, the external chitin of the body and the appendages having been crushed beforehand in order to hasten the action of the NaOH on the tissues proper. The solution, after cooling, was transferred to a separatory funnel, where it was acidified with HCl and extracted repeatedly with liberal amounts of ether. The collected ether fractions were filtered into a weighed container, the ether was evaporated, and the ether extract was dried for 1 hour at 60° C. and weighed. During these procedures the chitin remained undissolved. It was collected; thoroughly washed with dilute NaOH, HCl, and water; dried; and weighed. This was possible, however, only in the case of the crabs; the chitin of the external parasites is present in too small amounts to allow a satisfactory quantitative determination.

According to the outlined procedure, it was possible to express the fat content of the crabs in percentage of the total dry substance and of the dry substance minus chitin. The latter calculation gives a fair, though not absolutely exact, estimate of the fat content of the tissues proper, since the inorganic substances of the tissues were not determined. No attempt was made to calculate the percentage of fat present in fresh animals, since preservation may have changed the weight of the specimens in an unpredictable way.

MORPHOLOGICAL OBSERVATIONS

Histologically, the liver of *P. pubescens* presents the three main types of cells that are recognized in the liver of decapods in general. By far the most numerous are tall, columnar cells with vacuolated cytoplasm—the cells commonly called "fat cells" in the literature. These are the cells in which reserve materials are stored and are the only hepatic cells in which we were able to demonstrate fat by the methods used. The second type, spoken of as a "ferment cell," is shorter and broader than the fat cell. Its cytoplasm and nucleus are practically confined to the stalklike proximal region, while the main portion is occupied by a single large vacuole. In cross-sections of liver tubules of *P. pubescens* the ferment cells are seen to be grouped exclusively on a single longitudinal ridge that projects into the lumen. The young cells (*Anfangszellen*), interspersed among the others, are recognizable by their smaller size and nonvacuolated, more intensely staining, cytoplasm. Ferment cells and young cells were always found to be fat-free.

Fat droplets could be demonstrated in the liver cells of both infested and uninfested crabs, and occasionally droplets of fat were observed outside the tubule or within its lumen. The intracellular droplets were somewhat variable in size, but usually they were small. If fat was

present in very large amounts, the cross-sections of the tubules, after treatment with osmic acid, appeared entirely black except for the ridge of ferment cells (Pl. I, Fig. 2; Pl. II, Fig. 5); but examination under higher power showed that in these cases the fat was actually deposited in innumerable small droplets.

In order to obtain a semiquantitative evaluation of the fat present in the liver, the following stages were differentiated:

Stage 1.—Only a few scattered fat droplets are demonstrable in the cross-section of a representative tubule.

Stage 2.—More fat droplets are present than in the previous stage, but distinctly less than in the following stage. This amount corresponds to that shown in Figure 2*b* of Robson (1911).

Stage 3.—This amount is shown in Plate I, Figure 2.

Stage 4.—The fat content is intermediate between stages 3 and 5.

Stage 5.—This, the maximum amount, is shown in Plate I, Figure 1.

It should be emphasized that this evaluation is fairly accurate, since the various liver tubules of a given specimen showed a reasonable degree of uniformity in their fat content.

The various roots of a given parasite, on the other hand, were much less uniform in their fat content (Pl. II, Fig. 5). The average impression gained from several slides was used to classify the fat content of a parasite's root system according to the following stages: stage 1, fat-poor; stage 2, medium fat content; and stage 3, high fat content. These stages do not correspond to those employed for the liver, since the roots were usually considerably poorer in fat than the liver of the host.

In addition to the parasites recorded in Tables 1 and 2, a general study of the fat content of the complete root systems of three parasites was performed. The root system was isolated from the liver tubules of the host by dissection and then treated with osmic acid. It was found that the bulbous tips of the roots were all fat-free and that fat droplets were only demonstrable some distance from these terminations.

The results of our morphological observations are summarized in Tables 1

TABLE 1

RELATIVE FAT CONTENT OF LIVER OF NORMAL AND PARASITIZED MALE *Pagurus* AND OF ROOTS OF *Peltogaster*

Crabs		Parasites		
Size (Mm.)	Fat Content of Liver (Stage No.)	External Sacs per Host (No.)	Size (Mm.)	Fat Content of Roots (Stage No.)
	A. Normal Crabs			
11	4	0	.....	.....
11	4	0	.....	.....
11	4	0	.....	.....
19	5	0	.....	.....
	B. Parasitized Crabs			
8	3	1	8	3
10	1	1	8	1
11	1	1	11	1
13	3	1	13	2
13	2	1	14	3
18	3	1	8	3
12	3	Scar	.....	3

and 2. It is evident that the liver of normal females was, on an average, richer in fat than that of normal males and that in both sexes the presence of *Peltogaster* caused a noticeable decrease in fat content. The size of the parasite seemed to have little influence upon the degree of fat depletion.

Fat droplets could always be demonstrated in the roots, but the degree of fat accumulation in these organs seemed to be influenced little, if at all, by the size of the host or of that of the parasite.

The external sacs of thirteen parasites varying in size from 2.5 to 14 mm. were also sectioned and stained for fat. The smallest parasite was entirely fat-free. Beginning with a size of 3.5 mm., the external parasite showed some fat in the ovarian eggs; but in all cases such eggs contained only small amounts. In contrast, eggs and developing embryos present in the mantle cavity of mature parasites all showed an abundant supply of relatively large fat drops. This is rather surprising, since, after expulsion from the ovary and following fertilization, the eggs develop in a brood chamber, where it seems hardly likely that they could accumulate new reserve substances. It must be assumed that this fat results from chemical processes; or at least this fat becomes morphologically demonstrable through chemical processes that have, as their substrate, material accumulated in the egg during its development in the ovary—material, however, that could not be differentiated by the methods used.

TABLE 2

RELATIVE FAT CONTENT OF LIVER OF NORMAL AND PARASITIZED FEMALE *Pagurus* AND OF ROOTS OF *Peltogaster*

Crabs		Parasites		
Size (Mm.)	Fat Content of Liver (Stage No.)	External Sacs per Host (No.)	Size (Mm.)	Fat Content of Roots (Stage No.)
	A. Normal Crabs			
9	5	0	.....	.....
12	5	0	.....	.....
13	4	0	.....	.....
13	5	0	.....	.....
13	5	0	.....	.....
	B. Parasitized Crabs			
8	3	1	8	2
10	2	1	7	2
12	2	2	11, 3.5	1
14	3	2	12, 11	2

It seems fairly obvious that the fat present in the developing embryos represents a reserve material. This is borne out by observations on fully developed free-swimming nauplii. They showed a marked decrease in fat content—a condition quite understandable if one keeps in mind that the nauplii never feed, lacking, as they do, all trace of an alimentary canal.

CHEMICAL OBSERVATIONS

The fat determinations by chemical methods are summarized in Tables 3 and 4. They indicate that more fat is stored in normal females than in males and that in both sexes less fat is present in parasitized than in normal crabs. Taking as the best basis for comparison the figures that give the chemically determined fat in percentage of dry weight minus chitin, we can state that the fat content of normal females averages 16.5 per cent, whereas parasitized females average only 7.0 per cent. Similarly for males, the fat content of uninfested, 12.2 per cent, is reduced to an average of 5.9 per cent in parasitized specimens. The more pronounced depletion of fat reserves in females is probably attributable to the fact that parasitized females suffer a practically complete atrophy of the ovaries (bulky organs of considerable fat content), while parasitized males undergo no castration (Reinhard, 1942).

It is well to remember, however, that the figures for the fat content of the parasitized animals are not so exact as those for the normal crabs. Both the absolute weight of the dry substance and the ether extract are somewhat too high, owing to the fact that the roots of *Peltogaster* re-

mained in the body of the host. To attempt to separate the roots without losing host tissue would obviously have been futile. We do not believe that this source of error will invalidate the results of the determinations, especially since corroborative evidence for their reliability is seen in the fact that they point to changes in the fat content of the whole body paralleling closely those found with morphological methods on the liver.

The fat content of the external sacs of the parasites was extremely high, varying from 21.6 to 35.7 per cent of dry weight. The sacs studied were mostly of average adult size. It will be remembered that the morphological fat studies showed the great majority of the fat droplets to be in developing eggs and embryos. The ether-extract determinations seem to support the view that the fat which becomes visible in embryos may be derived from masked fat, that is, fatty substances which escape the morphological methods. The supposition that perhaps a large part of the chemically determined fat is located in other tissues than developing embryos seems inescapable. Although the proportions in weight between mantle tissues, ovary, and developing embryos is not known, it appears likely that impossible figures would result if the greatest part of the fat found in the external sac were attributed to the developing embryos in the mantle cavity.

TABLE 3

CHEMICALLY DETERMINED FAT CONTENT OF NORMAL AND PARASITIZED MALE *Pagurus* AND OF THE EXTERNAL SAC OF *Peltogaster*

Crabs							External Parasites			
				Ether Extract					Ether Extract	
No. of Animals	Size (Mm.)	Dry Weight (Gm.)	Chitin (Per Cent)	Gm.	Percentage of Total Dry Weight	Percentage of Dry Weight Less Chitin	Animal No.	Dry Weight (Gm.)	Gm.	Percentage of Dry Weight
	A. Normal Crabs									
4	15–16	3.343	53.4	0.190	5.67	12.19	0	.....	.....	.....
4	11	1.486	48.5	0.088	5.92	11.49	0	.....	.....	.....
4	11–12	2.253	50.0	0.123	5.46	10.92	0	.....	.....	.....
4	13–14	3.042	50.0	0.215	7.06	14.12	0	.....	.....	.....
	B. Parasitized Crabs									
4	11	1.180	50.0	0.028	2.37	4.74	4	0.153	0.034	22.1
2	10–12	0.541	48.6	0.024	4.43	8.63	4	0.082	0.022	26.8
4	11–13	1.787	40.2	0.100	5.60	9.26	4	0.177	0.054	30.5
3	9–10	0.566	50.0	0.031	5.48	10.96	3	0.059	0.013	22.1

DISCUSSION

In view of the bearing the present studies have on the complicated problem of parasitic castration, and particularly

since Smith's theory to account for feminization of parasitized males rests on "fat increase" as the very keystone—a theory that has gained rather widespread acceptance—the authors feel that the discussion should be presented at some length and, furthermore, should critically review other metabolic changes produced under the influence of such parasites as *Sacculina* and *Peltogaster*. In this way it is hoped that our registration of disagreement with certain commonly accepted statements and our placing of fresh emphasis on elements that have been rather neglected in other reviews of the problem will stimulate investigation along lines that should yield fruitful results.

To begin, then, the present paper shows that the fat content of the body of *P. pubescens* infested with *P. paguri* is definitely lower than that of normal hermit crabs. What is the purport of this in relation to the findings of Smith and Robson? One's first reaction is to accept their studies as demonstrating fat increase in the sacculinized hosts they studied, denying, however, that this must be taken as an effect characteristic of rhizocephalan parasitism in general. Certainly, these studies on *Peltogaster*, coupled with the observation of Pierre on *Septosaccus*, show clearly that there are cases of this type of parasitism where the fat resources of the host are diminished.

If, then, we set up two main types of effect, it is very tempting to try to correlate these either with different classes of parasites or with different types of hosts.

TABLE 4

CHEMICALLY DETERMINED FAT CONTENT OF NORMAL AND PARASITIZED FEMALE *Pagurus* AND OF THE EXTERNAL SAC OF *Peltogaster*

Crabs							External Parasites			
				Ether Extract					Ether Extract	
No. of Animals	Size (Mm.)	Dry Weight (Gm.)	Chitin (Per Cent)	Gm.	Percentage of Total Dry Weight	Percentage of Dry Weight Less Chitin	Animal No.	Dry Weight (Gm.)	Gm.	Percentage of Dry Weight
	A. Normal Crabs									
4	11	1.469	44.6	0.139	9.46	17.09	0	.....	.....	.....
4	10	1.278	46.6	0.093	7.28	13.61	0	.....	.....	.....
3	11–12	1.514	46.1	0.138	9.11	16.92	0	.....	.....	.....
3	11	1.248	53.2	0.106	8.48	18.54	0	.....	.....	.....
	B. Parasitized Crabs									
4	10–12	1.404	54.3	0.044	3.14	6.87	4	0.174	0.052	29.9
4	10	0.968	54.6	0.035	3.62	7.46	4	0.090	0.022	24.4
3	9–11	0.874	46.7	0.023	2.67	4.94	3	0.028	0.010	35.7
3	10–12	1.057	47.7	0.048	4.52	8.69	6	0.097	0.021	21.6

A sacculinid (*Drepanorchis*) is involved in one case, peltogastrids (*Septosaccus* and *Peltogaster*) in the other; anomurans (*Carcinus, Inachus*) in one case, brachyurans (*Diogenes, Pagurus*) in the other. Still more provocative is the fact that the sacculinid causes marked modifications of the secondary sexual characters of the male hosts, while *S. cuenoti* and *P. paguri* cause little, if any, external modifications of their respective hosts: *D. pugilator* (Pérez, 1932) and *P. pubescens* (Reinhard, 1942). However tempting apparent relationships of this sort may seem, they must be discounted, at least for the present; and arrangement of material in a categorical manner must await the study of more cases. Moreover, with regard to the external modifications, it may be that such modifications are not conditioned by fat changes but that both are the result of some other, not yet determined, factor or factors.

We cannot, however, accept the reports of Smith (1911, 1913) and Robson (1911) as having unequivocally demonstrated fat increase in parasitized crabs—at least not to the extent claimed. It is questionable whether the differences between their results and ours are really as pronounced as appear at first glance. Smith and Robson, using histological methods, found an increased deposition of fat droplets in the liver tubules, and the former likewise showed by chemical methods that the fat percentage of livers in infested *Carcinus* was higher than in normal ones. These observations, while contradictory to our histological findings, obviously do not prove that the fat content of the entire body was higher, or even necessarily that the total amount of fat deposited in the liver of an infested animal was in excess of that in an uninfested one. E. Fischer (1928) has shown that a rather pronounced reduction in the amount of liver tissue takes place in *Carcinus* as a result of sacculinization. It is therefore altogether possible that, despite an increase in fat percentage for the liver tissue that remains, the total fat of the entire liver, as well as the whole animal, may be less than normal.

Hughes, it is true, presents evidence of an increase in total fat content from 1.04 to 1.6 per cent in the case of male *Upogebia* parasitized by *Gyge*, although the fat content of infested females was considerably lower than that of ovigerous females. It should be pointed out that these figures express fat in percentage of wet weight of formalin-preserved specimens and cannot, therefore, exactly be compared with figures based on dry weight. One cannot help mentioning, in passing, that a method based on wet weight, when the relative fluid content of normal and parasitized animals is unknown, may be of questionable accuracy. At any rate, the differences that exist between a purely external sucking parasite, as is *Gyge*, and a rhizocephalan with roots that invade the whole body of the host are so great in nurture, as well as in nature, that identity of effects is not to be expected.

Geoffrey Smith's theory of metabolic stimuli, namely, that the parasite forces the host to elaborate more fatty material than usual in order to furnish food for the parasite and that this change in metabolism brings about sex reversal in male hosts is still subscribed to by Hughes, writing as late as 1940, although several investigators (see especially Brinkmann, 1936) have clearly shown that Smith's hypothesis can hardly explain all facts. It seems to us that this theory encounters still more difficulties than hitherto brought against it, if the facts known about fat metabolism are considered critically. It is certainly true that all the body substance of the para-

site is built from material extracted from the host and that this organism, so dependent on the host, is extremely rich in fat. But the assumption that the fat of the host serves directly as food for the parasite is, although possible, quite unproved.

Smith bases his view on two observations: (1) that the roots of the parasites contain "yolk" material which he considers identical with the fatty droplets of the host liver and (2) that the blood of males and castrated females shows a color that is characteristic of the blood of females with maturing ovaries, the blood of such females being very rich in fat.

If considered from a purely physiological viewpoint, these observations do not appear convincing. A direct resorption of the host fat droplets has never been demonstrated; as a matter of fact, the bulbous root tips which conceivably might be the most actively resorbing parts of the roots were, at least in the case of *Peltogaster*, always entirely devoid of fat. This does not, of course, necessarily exclude the possibility that fatty substances are resorbed from the host blood; but it indicates that, if this is the case, the fat is perhaps first broken down into soluble compounds and resynthesized inside the roots—a process that could be compared to fat resorption in higher animals. It is, however, equally possible that the fat is synthesized in the roots from other substances than fat. On cytological grounds E. Fischer (1927) and Dornesco and Fischer-Piette (1931) have already concluded that the roots of *Sacculina* are not primarily absorptive organs but that the nutritive substances coming from the crab are herein changed before reaching the parasite proper.

As for the alleged fat increase in the blood of the hosts, this has never been demonstrated chemically. Such a check would appear highly desirable, inasmuch as Robson's observation of the changed color of the blood of parasitized *Inachus*, as interpreted by Smith, is open to an alternate explanation. Smith himself points out that the pigments of the blood are deposited in the skin after a molt, that parasitized *Inachus* do not molt as a rule, and that this might be the reason for pigment increase in the blood of these animals. He seems then to assume tacitly that there is a rigid ratio between pigments and fat. Could it not equally well be that it is only the pigments that accumulate, since they are not used, whereas the fat content might be unchanged or even lower than normal? In other words, could not simply the ratio between these two groups of substances be changed? Such an alternate assumption would appear just as likely as Smith's, especially in view of recent experiments (Drilhon and Pora, 1936) demonstrating considerable change in the ratios between various inorganic substances, and also blood proteins, in sacculinized crabs.

Another assumption frequently met with in the literature dealing with changes observed in sacculinized crustaceans is that these changes are due to an excessive loss of food occasioned by the nutritional requirements of the parasites ("Gargantuan appetite," according to Robson). Again it should be pointed out that a comparative physiologist would approach this question with more caution than a morphologist, so long as there are no data available concerning the relative rate of metabolism of host and parasite. This, after all, seems to us to be the only decisive point. A host with a high rate of metabolism and having an ample food supply should be able to maintain its own metabolism and that of even a large parasite, provided the metabolic level of the latter is low. On the other

hand, a host with a low rate of metabolism and accustomed to only meager food intake might have greater difficulty in providing enough food both for itself and for a large parasite with high metabolic requirements. But, even in this case, it is hard to see why increased food consumption would not help to prevent the changes that are commonly attributed to slow starvation. Certainly, the evidence from other fields of parasitology is, on the whole, unfavorable to the view that food robbery is of any great importance. Studies on the possibility of protozoan and helminthic metabolism influencing the metabolism of the host, when there is disturbance of the latter, point more toward toxic influence as the cause of these changes.

In sacculinized crabs there are indications that toxic influences are at work. Drilhon's findings of well-marked biochemical changes in the blood (1936) and the muscular tissues (1937), which indicate a metabolic disequilibrium of the host, could be interpreted in this way. These and the other biochemical changes that have been reported (cf. papers previously cited) involving fat, glycogen, mineral substances, proteins, physicochemical constants of the blood, etc., all point to widespread metabolic disturbances that elaboration by the parasite of substances toxic to the host animal could readily explain. This is all the more likely because Lévy (1923, 1924) has established the presence in *Sacculina* of substances that are toxic to *Carcinus*—observations which, strangely enough, have had very little influence, in the years since, on the conceptions expressed by most biologists regarding the broad problem at hand.

SUMMARY

1. With morphological methods the fat content of the liver of *Pagurus* parasitized by *P. paguri* is shown to be definitely lower than that of normal crabs.

2. Fat determinations of entire crabs by chemical methods likewise show that much less fat is present in parasitized than in normal crabs.

3. Normal females are richer in fat than normal males, but females suffer a greater amount of fat reduction through parasitization.

4. The external sac of *Peltogaster* acquires increasing amounts of fat as the parasite matures, extreme amounts being visible in eggs and developing nauplii in the mantle cavity.

5. The roots of *Peltogaster*, except near their terminations, always possess fat, but the amount is quite variable even in the same root system.

6. The hypothesis proposed by G. Smith to explain the effects of sacculinization is adversely criticized from the standpoint of comparative physiology, and constructive proposals are offered for future investigation. It is pointed out that the elaboration of toxins by the parasite might explain the observations and that the indications concerning the presence of such toxic substances are strong enough to warrant further work along these lines.

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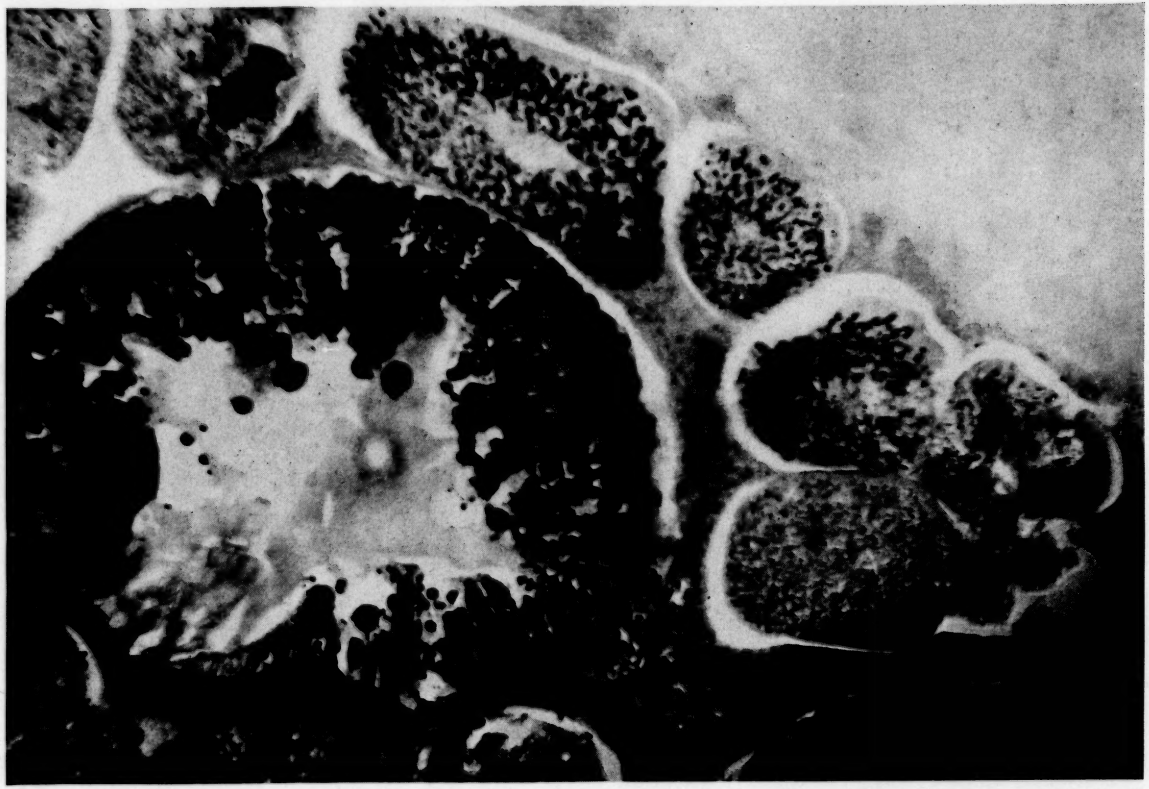
PLATE I

PLATE II



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PLATES I–II

PLATE I

Photographs demonstrating fat content of the parasite *P. paguri* and its host *P. pubescens*. The sections, prepared by the freezing method, were treated with osmic acid. Fat appears black.

FIG. 1.—Liver tubules of normal crab showing maximum fat deposition, designated as stage 5. ×80.

FIG. 2.—Liver tubule of parasitized crab surrounded by roots of *Peltogaster*, with portions of three other tubules appearing at the margins of the figure. The degree of fat deposition in the liver corresponds to stage 3, while the roots are relatively fat poor. ×85.

FIG. 3.—Cross-section of a single root of *Peltogaster* showing high fat content. ×320.

FIG. 4.—Ovarian portion of visceral mass of the external sac of a mature *Peltogaster* (*at left*) and mantle cavity containing developing embryos (*at right*). Note low fat content of ovarian eggs as compared to high fat content of developing embryos. Clear areas are due to loss of embryos during preparation of the frozen sections. ×95.

PLATE II

FIG. 5.—Roots of *Peltogaster* and one liver tubule of *Pagurus* treated with osmic acid. Roots show variations in fat content, while fat content of liver is of the degree designated as stage 3. Note characteristic ridge of fat-free ferment cells in the liver tubule. ×115.

THE METABOLISM OF THE EXCISED BRAIN OF THE LARGEMOUTHED BASS (HURO SALMOIDES) AT GRADED TEMPERATURE LEVELS[1]

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THERE is much information in the literature concerning the metabolism of excised mammalian brain (Quastel, 1937, 1939; Corcoran and Page, 1940) but little relating to the metabolism of the brain in other forms. In particular, the vertebrate heterotherms have received scant attention from this point of view. Thus in the recent literature the papers of Rosenberg (1935) on the oxygen consumption of frog brain and of Palladin and Rashba (1935) on oxygen consumption and ammonia content of frog, toad, and lizard brain appear to be the chief relevant material. This investigation of fish-brain metabolism was undertaken to extend a general study of the effects of temperature on the metabolism of isolated tissues and to provide additional data on the tissue metabolism of groups other than the Mammalia. Furthermore, the reports that the metabolism of intact fish, unlike that of intact mammals, is not augmented by administration of desiccated thyroid (Etkin, Root, and Mofshin, 1940) or of epinephrine (Smith and Matthews, 1942) warrant investigation of fish-tissue metabolism. The black bass was chosen because it was a readily available vertebrate heterotherm with a brain large enough to permit measurement of metabolism *in vitro* by standard methods.

[1] Supported in part by a grant from the John and Mary R. Markle Foundation.

MATERIAL AND METHODS

ANIMALS

The largemouthed black bass, *Huro salmoides* (Lacépède) (Hubbs and Bailey, 1940) has a wide habitat range in California. It is frequently found in warm lakes and in the sluggish waters of the river systems of the central valleys (Brown, 1939). In winter, however, the temperature of these waters may drop to about 4° C. (Felin, 1940). The specimens used were obtained from Searsville Lake, an artificial reservoir about 4 miles southwest of the Stanford campus. This lake is about $\frac{3}{4}$ mile long and $\frac{1}{4}$ mile wide, with a maximum depth during the summer of about 8 meters. The surface temperature during the period of collection of fish (July–September, 1942) ranged from 22° to 24° C. Temperature at a depth of 8 meters was 21° C. late in July. Extensive data on water temperature taken during 1938 show maximum surface temperatures of about 25° C. and minimum deep temperatures of about 20° C. from July to September (Felin, 1940). Although some stratification develops in the lake, on the whole the water shows the thermal instability characteristic of shallow lakes. According to the available data, the lowest surface temperature reached in winter is about 4° C. Searsville may thus be classified as a "tropical" lake (cf. Whipple, 1927). Further data on the limnology of Searsville are

given in the theses of Scott (1927) and of Felin (1940).

Thirty-eight fish were used. These were transported to the laboratory and maintained overnight in aerated lake water. The animals ranged in length from 9 to 15 inches.

PREPARATION OF TISSUE

The brain was removed immediately before use. It was freed from blood and nonnervous tissue, transferred to a moist chamber, and minced with forceps on a glass plate. As the mince promptly shook to pieces in the Warburg vessel, fineness of slicing was not critical. Aliquots were weighed on a microtorsion balance to obtain wet weights and then transferred to respirometer vessels for metabolic measurements or to crucibles for the determination of dry weight. The latter samples were dried to constant weight in an electric oven at 105° C. When several fish were available at one time, the brains were pooled before weighing. Time between death of the animals and the beginning of metabolic measurements was kept quite constant at 30 minutes (cf. Field, Belding, and Martin, 1939).

OXYGEN CONSUMPTION

The oxygen consumption was determined manometrically by the direct method of Warburg, with the precautions suggested by Dixon (1934) and by Field, Belding, and Martin (1939). The medium was amphibian Ringer's solution, buffered at pH 7.35 with a mixture of sodium phosphates in a final concentration of 0.007 M containing 0.14 per cent glucose. The gas phase was oxygen. Four thermostats were available, two of which were equipped with refrigeration units. Thus it was possible to make simultaneous measurements of oxygen consumption on tissues from one animal at four different temperature levels. Oxygen consumption is expressed in terms of cubic millimeters at normal pressure and temperature per milligram dry weight per hour (Q_{O_2}). Under the conditions of these experiments the decline in Q_{O_2} of minced bass brain is negligible (less than 10 per cent) during the first hour of a run. During this time period there is no decrease at all in the Q_{O_2} of rat brain cortex. All the data given in this paper are calculated from such periods of constant Q_{O_2}. Data on the water content of bass brain are given in Table 1.

TABLE 1

WATER CONTENT OF WHOLE BRAIN IN ELEVEN BASS

Whole brain removed and minced immediately on glass plate in moist chamber. Minced brain weighed on microtorsion balance, transferred to crucibles, and dried 24 hours in an electric oven at 110° C.

Mean percentage water	81.85%
Range	79.88–83.72%
Standard deviation	1.068%
Standard error of mean	0.322%
Coefficient of variation	1.305
Mean W/D ratio*	5.52

* W/D ratio = Wet weight/Dry weight. The Q_{O_2} on a wet-weight basis, multiplied by this factor, gives the Q_{O_2} on a dry-weight basis.

AMMONIA PRODUCTION

The ammonia production was determined by a slight modification of the method of Russell and Wilhelmi (1941). The ammonia present in some respirometer vessels was measured at the end of the period of thermo-equilibration (initial values) and in others after determination of oxygen consumption. This involved the use of vessels with two side arms. One arm contained 0.5 ml. of N H_2SO_4 and the other 0.5 ml. of 40 per cent NaOH. At the end of the thermo-equilibration or the experimental period the H_2SO_4 was added. After 10 minutes the vessel was removed, connected to an

aeration apparatus, and the NaOH added. The ammonia was then aerated into 0.05 N H_2SO_4 and the nitrogen determined with a photoelectric densitometer after nesslerization. An average recovery of 97 per cent of the ammonia in known samples was obtained by this method.

RESULTS AND DISCUSSION

OXYGEN CONSUMPTION

The rate of oxygen consumption of minced whole bass brain at graded temperature levels ranging from 5° to 40° C. is shown in Figure 1. For comparison, a similar curve obtained on mammalian cerebral cortex slices (rat), taken from a previous study (Fuhrman and Field, unpublished), is also given in Figure 1.

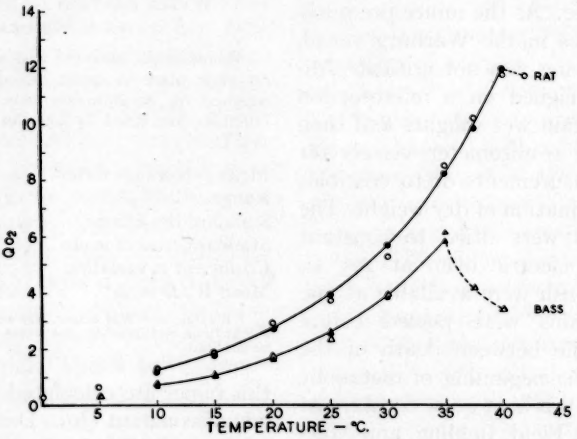

FIG. 1.—Graph showing Q_{O_2} of excised rat (*circles*) and bass (*triangles*) brain as a function of temperature. Open symbols represent experimental values; closed symbols represent values calculated from the formulas given for log Q_{O_2} as a function of temperature in section on temperature coefficients.

It is shown in Figure 1 that the curve of Q_{O_2} as a function of temperature is similar in shape for bass and rat brain, except that in the case of the bass the "optimum temperature" is displaced about 5° C. down the temperature scale. It is also shown that at a given temperature the absolute Q_{O_2} of rat cortex slices is always higher than that of minced bass brain. Furthermore, if oxygen consumption be calculated on the wet-weight basis, the rates of respiration of rat cortex remains the higher. It seems probable that this difference is due in part to the inclusion of a greater proportion of white matter in the preparation of bass brain used (in the mammalian brain the Q_{O_2} of white matter is lower than that of gray matter [Quastel, 1937, p. 374]). Furthermore, in our experience, the Q_{O_2} is lower and less constant in minced than in sliced brain.

The optimum temperature for the respiration of minced bass brain is about 35° C. (Fig. 1); hence in the body-temperature range of homeothermic animals (cf. Pembrey, 1898) the oxygen consumption of bass brain would be considerably depressed. This may indicate qualitative differences in the respiratory enzymes functioning in heterotherm and homeotherm brains under these conditions (cf. Deighton, 1933).

Since the habitat temperature (and

therefore the body temperature) of the bass used averaged about 23° C. and did not rise above 25° C., the maximum oxygen consumption of the brain *in vitro* occurred at 10° or 12° C. above the usual body temperature. Interesting in this connection is the finding of Belding, Field, Weymouth, and Allen (1942) that the optimum temperature for the respiration of excised midgut gland of the kelp crab (*Pugettia producta*) is about 25° C., while the habitat temperature of these animals is about 15° C. It might be inferred from these data that there is some approximate relation between habitat temperature and the optimum temperature for tissue respiration, although much more evidence would be required to establish such a hypothesis. An interesting parallel to these results is afforded by the work of Doudoroff (1938), which showed that certain marine fishes (in particular, *Girella*), when offered a wide range of habitat temperatures, tend to select a level which is relatively high when compared to the usual habitat temperature (about 26°–27° C. for fish from a mean habitat temperature of about 17° C.). Furthermore, Sumner and Doudoroff (1938) have shown that acclimatization of marine fish at 30° C. resulted in increased resistance to heat, as indicated by prolonged survival time at high temperatures. Experiments on Searsville bass, taken during the winter, are planned. These will show whether the "optimum" temperature for excised brain Q_{O_2} decreases with diminution in habitat temperature.

TEMPERATURE COEFFICIENTS

To determine whether the variation in the oxygen consumption of excised bass brain with change in temperature could be represented by the Arrhenius equation,

$$\mu = \frac{4.56(\log R_2 - \log R_1)T_1T_2}{T_2 - T_1},$$

where R_1 and R_2 are the rates of oxygen consumption (Q_{O_2}) at the absolute temperatures T_1 and T_2 and μ is a constant called the "thermal increment" or "temperature characteristic," log Q_{O_2} was plotted as a function of the reciprocal of the absolute temperature. If the Arrhenius equation holds, this function will be

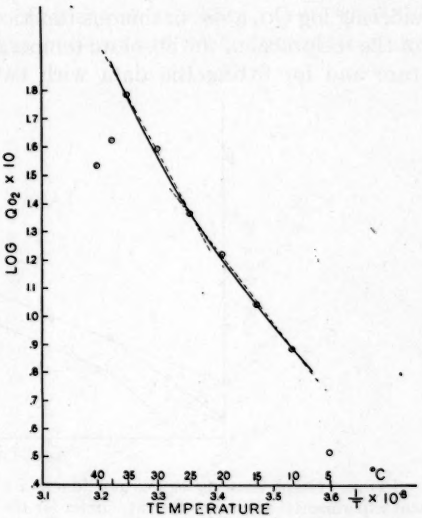

FIG. 2.—Graph showing log Q_{O_2} of bass brain as a function of the reciprocal of the absolute temperature. The solid curve shows log Q_{O_2} as a continuous function. The broken lines represent attempts to fit straight lines to values of Q_{O_2} at 25°, 30°, and 35° C. and at 10°, 15°, and 20° C.

linear (cf. Buchanan and Fulmer, 1930, p. 44).

In our opinion the most reasonable interpretation of the relation shown in Figure 2 is that, over the temperature range 10°–35° C., log Q_{O_2} is a continuous function of the reciprocal of the absolute temperature and that the slope of the curve varies with temperature. Since the value of μ is determined by this slope, it follows that μ is not a constant in this case. While it is possible to fit the values of log Q_{O_2} corresponding to 25°, 30°, and 35° C. fairly well with one straight line

and those corresponding to 10°, 15°, and 20° C. with another (broken lines in Fig. 2), the validity of these lines rests on only three points in each instance. Furthermore, the slopes of these lines do not differ very greatly. Under these circumstances the standard errors of the slopes are too great to show significant differences between them. The case for considering log Q_{O_2} a discontinuous function of the reciprocal of the absolute temperature and for fitting the data with two straight lines is therefore a doubtful one on statistical grounds in the present instance. However, for comparison with data in the literature treated in this way, it may be stated that the broken lines in Figure 2 have slopes such that μ for the range 25°–35° C. is 17,840 and for the range 10°–20° C. is 12,740. The value of log Q_{O_2} at 5° C. does not lie on the curve or curves determined by the other points.

For theoretical—and controversial—discussion of the significance of such data the reader is referred to Crozier (1924–25), Cameron (1930), Buchanan and Fulmer (1930), Stier (1933), Bělehrádek (1935), Burton (1936), Hoagland (1936), and Heilbrunn (1937).

Since it appeared that the value of μ varied with change in temperature (Fig. 2), the constancy of the van't Hoff coefficient, Q_{10}, as given by the formula

$$\log Q_{10} = \frac{10(\log R_1 - \log R_2)}{t_1 - t_2}$$

—where R_1 and R_2 are the rates of oxygen consumption (Q_{O_2}) at temperatures t_1 and t_2 (degrees centigrade—was tested by plotting log Q_{O_2} as a function of temperature in degrees centigrade. The curve so obtained is given in Figure 3.

It is shown in Figure 3 that log Q_{O_2} appears to be a linear function of the temperature in degrees centigrade over the range 10°–35° C. for the excised bass brain and 10°–40° C. for the excised rat brain (unpublished data of Fuhrman and Field, shown for comparison). The straight lines drawn in Figure 3 were fitted to the data by the method of least squares. Such a linear relation indicates that Q_{10} is constant over the temperature range involved (cf. Buchanan and Fulmer, 1930, p. 38). The equations corresponding to these curves are given below. For the rat brain:

$$\log Q_{O_2} = -0.2146 + 0.03226t\ ; \quad (1)$$

for the bass brain:

$$\log Q_{O_2} = -0.4953 + 0.03605t\ , \quad (2)$$

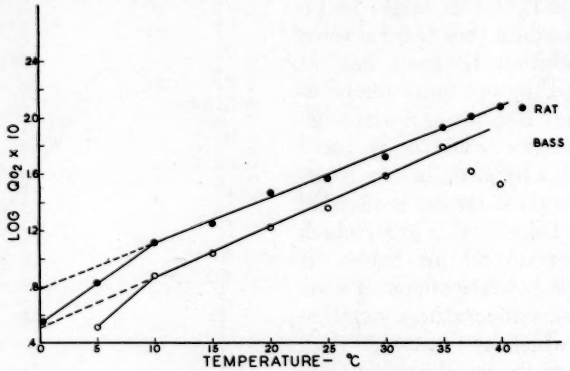

FIG. 3.—Graph showing log Q_{O_2} as a function of the temperature in degrees centigrade. Triangles represent experimental values for the rat; circles for the bass. The straight lines were fitted by least squares.

where t = temperature in degrees centigrade. The corresponding values of Q_{10} are antilog 0.3226, or 2.102, for the rat brain and antilog 0.3605, or 2.294, for the bass brain. Thus, while the rat brain shows a higher rate of oxygen consumption (Q_{O_2}) over the temperature range 10°–30° C., the rate of bass brain respiration is more accelerated by rise in temperature in this range.

It is shown in Figure 3 that there is a break in both of the curves at 10° C. The validity of this observation is increased by the dual occurrence. Its significance we do not know.

COMPARISON OF RATES OF RESPIRATION IN THE EXCISED BASS BRAIN AND IN THE INTACT BLACK BASS

The rate of oxygen consumption of intact black bass fingerlings (body weights ranging from 13 to 68 gm.) has been measured by Wiebe and Fuller (1933). They reported a value of 2–3 for the Q_{10} of oxygen consumption over the interval 15°–25° C., which agrees with our finding of 2.29 for the Q_{10} of bass brain respiration over the interval 10°–35° C. Their results, converted to a ratio in which the rate of oxygen consumption at 15° C. is equal to 1.00, are given in Figure 4. Our data on the respiration of excised bass brain, converted to a ratio in which Q_{O_2} at 15° C. = 1, are plotted in the same graph.

It is shown in Figure 4 that there is much similarity in the shape of the curves and rather close coincidence with respect to the position in the graph, when the oxygen consumption of the intact animal and that of the minced brain are plotted, in terms of the above ratios, as functions of temperature. The agreement seems rather good when the disparities in size (therefore in age), habitat, and the like between their fish and ours are considered. It seems reasonable to conclude that such agreement constitutes evidence that the experiments *in vitro* are physiological, i.e., that they do depict metabolic events in the intact organ or in the body. This view is reinforced by the similar findings of Fox and Wingfield (1937) on some other forms.

AMMONIA PRODUCTION

It is shown in Figure 1 that, when the Q_{O_2} of bass or of rat brain is plotted as a

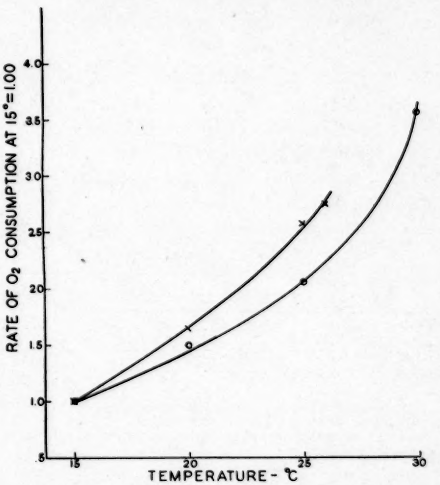

FIG. 4.—Graph showing oxygen consumption of bass fingerlings (*circles*) (Wiebe and Fuller, 1933), for comparison with that of excised brain (*crosses*). Oxygen consumption expressed on a scale such that the rate of oxygen consumption at 15° C. equals 1.00.

function of temperature, the curves obtained exhibit a single maximum. Although there has been much investigation on the point, there is still no certainty as to the cause of the diminution in Q_{O_2} at temperatures above the optimum (cf. Bělehrádek, 1935; Heilbrunn, 1937). Possibly it is associated with increased catabolism of protein or other nitrogenous compounds involved in the catenary series of respiratory reactions or in cell structure in some essential way (cf.

Gray, 1928). These considerations, together with the finding (in routine measurements of the pH of the contents of the respirometer vessels with a glass electrode) that at 37.5° C. there was an increase in pH in the medium containing bass brain instead of the slight decrease observed with rat brain, led to this investigation of ammonia production. The results of ammonia determinations on the contents of respirometer vessels at graded temperature levels and after various time intervals are given in Table 2.

TABLE 2

AMMONIA PRODUCTION BY EXCISED BASS BRAIN IN MG. AMMONIA PER 100 GM. DRY WEIGHT OF BRAIN (MEANS)

Numbers in parentheses give number of animals used in calculation of mean values given.

	Temperature (°C.)				
	20	25	30	37.5	40
Control (initial)*...	60 (2)	.....	.....	63 (1)	.....
After 1 hour.....	.....	.....	.....	84 (2)	.....
After 2 hours.....	125 (4)	140 (4)	126 (3)	187 (8)	298 (2)
After 5 hours.....	.....	.....	.....	268 (2)	.....

* Controls taken at beginning of measurement of tissue respiration (zero time), ½ hour after death.

These figures can be converted to a wet-weight basis by dividing by 5.52.

It is shown in Table 2 that at the two temperature levels above 35° (i.e., above the "optimum" temperature for respiration in excised bass brain) the rate of ammonia formation is much greater than that at the three levels below 35°. Thus the rate of ammonia formation is increasing with rise in temperature in the range where the rate of oxygen consumption is decreasing. However, the ammonia production at 37.5° C. was not sufficient to account for the total pH increase in suspension media containing bass brain at this temperature. Possibly hydrolysis of phosphocreatine (Fiske and Subbarow, 1929; Kerr, 1935) or formation of amines may also be concerned.

The source of the ammonia formed during the maintenance of the brain *in vitro* is not known. Riebeling (1931, 1934) suggested that it is derived from adenylic acid, as Embden showed was the case in muscle (1930). Additional evidence for this view is afforded by the finding of Fainschmidt (1936) that the ammonia concentration in the brain of ground squirrels increases on awakening from hibernation and at the same time there is a decrease in adenylic acid. Krebs (1935) has shown that the brain contains an enzyme—glutaminase—capable of hydrolizing glutamine to glutamate and ammonia.

An increase in ammonia production with rise in temperature has been observed in intact fish by Kahn and Chekoun (1935), using *Carassius*. These fish, when maintained at 15°–16° C., showed an increase in the ammonia content of the brain of 97 per cent, and those maintained at 19°–20° C. of 197 per cent, over the level found in animals kept at 3°–4° C. It should be noted that our control values cannot be compared directly with those of Kahn and Chekoun, since our first determinations were not carried out until 30 minutes after the death of the animal (i.e., the time at which measurement of respiration was begun).

While these observations do not prove the hypothesis that the decline in the rate of tissue respiration at supramaximal temperatures is attributable to increased catabolism of some nitrogenous compound important in respiration, they are in harmony with such a view.

SUMMARY

1. The rate of oxygen consumption (Q_{O_2}) of minced brain of the large-mouthed black bass (*H. salmoides*), taken from a habitat temperature of 23° C., was measured at graded temperature levels ranging from 5° to 40° C. Thirty-

eight fish were used. The animals varied from 9 to 15 inches in length.

2. The Q_{O_2} of minced bass brain was compared with that of rat cerebral-cortex slices at corresponding temperature levels. The curves of Q_{O_2} as a function of temperature were similar in shape in the two cases. However, the "optimum" temperature for bass brain respiration was 35° C., while for rat brain respiration it was 40° C. A possible relation between habitat and optimum temperature in heterotherms was discussed.

3. When log Q_{O_2} of the bass brain was plotted as a function of the reciprocal of the absolute temperature, the curve obtained was not a straight line. Reasons were given for the inference that in this case log Q_{O_2} was a continuous function of the reciprocal of the absolute temperature, with varying slope.

4. When log Q_{O_2} of the excised brain was plotted as a function of the temperature in degrees centigrade, the curve obtained was a straight line over the range 10°–35° C. for the bass and 10°–40° C. for the rat. The equations corresponding to these curves are for rat brain:

$$\log Q_{O_2} = -0.2146 + 0.03226t ;$$

for bass brain:

$$\log Q_{O_2} = -0.4953 + 0.03605t ,$$

where t is temperature in degrees centigrade. Values of the van't Hoff coefficient, Q_{10}, which was constant for each animal in the above temperature ranges, were 2.102 and 2.294 for rat and bass brain respiration, respectively. Thus, while the respiration of rat brain was of greater rate at all temperatures, the respiration of bass brain was the more accelerated by rise in temperature.

5. Date on the respiration of black bass fingerlings, from the literature, were compared with our findings on the respiration of the excised brain when both were expressed as functions of temperature. It was shown that these curves were quite similar in shape over the limited range for which data were available.

6. It was found that the rate of ammonia production in the excised bass brain increased as the temperature rose above the optimum for respiration. It was therefore suggested that the decline in Q_{O_2} of bass brain at temperatures above 35° C. was associated with increased catabolism of some nitrogenous compound important in respiration.

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TOTAL AND TISSUE RESPIRATION IN RELATION TO BODY WEIGHT
A COMPARISON OF THE KELP CRAB WITH OTHER CRUSTACEANS AND WITH MAMMALS

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THE authors feel that many problems in physiology suffer from the provincialism of data and the restriction of view imposed by working on a single species and that a comparative attack might yield sounder and more generally applicable results. Although the phrase "comparative attack" suggests a discouragingly broad scope, it is thought that the cultivation of a smaller field

may not be unprofitable; and, accordingly, the staff of the department of physiology of Stanford University has attempted a modest program of joint comparative research, of which this paper is one of the fruits. This work has been carried on chiefly at the Hopkins Marine Station, located at Pacific Grove, California. As stated in an earlier paper (Belding, Field, Weymouth, and Allen, 1942), the first animal to be studied was the kelp crab, *Pugettia producta*, a common and easily available crustacean of this part of the coast. An investigation, now under way, of its life-history with special reference to form is designed to furnish a background for the various phases of its physiology. Since mammalian and tissue metabolism have for some time engaged the attention of the staff, this aspect of the physiology of the kelp crab early attracted our attention. We hope that the present study may illustrate the advantage of the comparative method.

Specifically, the present paper considers the oxygen consumption of the kelp crab and the effect upon this of oxygen partial pressure, sex, and body size. A comparison of respiration in the kelp crab with that of other crustaceans, with mammals, and with tissue respiration leads to certain general conclusions regarding the relation between respiration and body size.

METHODS AND MATERIALS

Kelp crabs, *P. producta* (Randall), were obtained from the kelp beds near the Hopkins Marine Station. Adult and immature crabs covering as wide a range of size as possible (from 1 to over 300 gm. total weight) and of both sexes were used. They were held in the station aquaria for a few days only and were not fed for at least 24 hours before respiration determination. The relation of body weight to length in this species is shown in Figure 1 of Belding *et al.* (1942).

The oxygen consumption of the crabs was measured in a constant-flow apparatus which provided for the sampling of the inflowing and outflowing water. The oxygen content of the sea water was determined by Winkler's method (Winkler, 1889; Allee and Oesting, 1934), and the amount of oxygen consumed was calculated from the difference in oxygen content and the rate of flow.

The crab was placed in the respiration chamber; and after a 1-hour equilibration period, which also served to cover the stage of exploratory activities of the animal, determinations of the oxygen content of the inflowing and outflowing water were made at intervals until the level of oxygen consumption during two successive periods was constant within 5 per cent. The oxygen content of the inflowing water remained so uniform that it was found unnecessary to make more than two or three measurements over a 2- or 3-hour test. The oxygen content of the effluent, however, was measured regularly every 20 minutes. The rate of flow of water through the chamber was measured at the time each sample was taken. By use of a water bath surrounding the respiration chamber and its connections the temperature of the animal and inflowing water was held constant at or near 15° C. Rates were converted to 15°, using a Q_{10} of 2.00, obtained in the work on tissue respiration. This is slightly (1°–3°) above the surface temperature of Monterey Bay for the summer months, during which the experiments were carried out.

The samples of water were taken in calibrated, glass-stoppered bottles holding approximately 135 cc. each. The precipitations and re-solutions were carried out in the original sampling bottles, and the titrations were made on the

whole sample with 0.01 N sodium thiosulphate thoroughly aged.

The tests on animals weighing less than 25 gm. were carried out with from two to seven individuals in the chamber at the same time, an effort being made to select crabs of similar size for any one test. In all cases the animals were observed during the run; and any results obtained during or immediately following activity, other than respiratory movements, were discarded. At the end of each test the animals were weighed and the total oxygen consumption expressed in terms of cubic centimeters of oxygen at normal temperature and pressure used per hour and as a weight-specific rate based on the animal's weight in grams.

The total wet weight of the intact animal, drained according to a standard procedure, was used. Although the exoskeleton presents a relatively large mass of inert material, it is impossible to determine its amount with sufficient accuracy to permit an adjustment of the respiratory rate; in this the practice parallels that in regard to the skeleton of mammals.

THE INFLUENCE OF OXYGEN PARTIAL PRESSURE ON OXYGEN CONSUMPTION

The literature of respiration in the invertebrates (cf. Keys, 1930; Tang, 1933) is full of contradictions regarding the effect of lowered oxygen tension on oxygen consumption. It seems probable, however, that in the higher invertebrates the rate tends to be constant over a fairly wide range of tensions. Since it was desired only to avoid tensions so low that the rate of respiration was affected, the lower part of the range was explored to determine the critical oxygen tension for *Pugettia*. Two methods were used: (1) the conventional method of placing the animal in an oil-sealed jar and at intervals withdrawing samples of water for oxygen determination, and (2) the flow method, in which the rate of flow of water through the respiration chamber was adjusted to give different partial pressures of oxygen. The results were consistent in showing that at oxygen partial pressures below 50 mm. Hg the oxygen consumption is markedly reduced. In the range between 70 and 50 mm. a moderate reduction was evident in most experiments. Above 70 mm., increase in oxygen partial pressure was not accompanied by an increased oxygen consumption. It was, therefore, considered advisable to set the lower limit of partial pressure to be used in determinations of normal resting oxygen consumption at or near 100 mm. Hg. This is in agreement with the work of Hall (1929) in which the critical tension for the puffer (*Tetraodon*) was found to be 100 mm. Hg and that for the scup (*Stenotomus*) 70 mm. Hg.

It may be pointed out here that the use of the unmodified Winkler method for determining the oxygen content of the water in these experiments does not exclude the possibility of error resulting from the presence of nitrites (Allee and Oesting, 1934). If sufficient nitrites were present, the error would lie in the direction of falsely high values for oxygen content. The good agreement between the results of the jar method and the constant-flow method suggests that no significant accumulation of nitrites occurred.

OXYGEN CONSUMPTION IN THE KELP CRAB

In Table 1 are given the body weight and the oxygen consumption, both total and weight-specific, for the thirty-four crabs studied. These data are the most extensive available, as far as known, for any invertebrate species. Inspection

shows that, although with increase of body size the total oxygen consumption increases, the weight-specific oxygen-consumption rate (oxygen consumed per unit of time and per unit weight of crab) decreases.

TABLE 1

OXYGEN CONSUMPTION IN THE KELP CRAB

No.	Length (Cm.)	Weight (Gm.)	Oxygen Consumption	
			Total (Cc./Hr.)	Rate* (Cc./Hr./Gm.)
	Males			
5.....	2.01	2.53	0.4296	0.16980
5.....	2.90	2.90	0.3626	0.12504
8.....	2.50	5.31	0.4938	0.09298
2.....	3.33	10.7	1.3698	0.12801
2.....	4.47	25.5	2.9851	0.11699
1.....	5.20	37.8	2.5085	0.06631
1.....	5.38	44.5	4.2480	0.09552
1.....	6.20	68.0	6.5400	0.09615
1.....	6.66	80.5	7.6469	0.09505
1.....	6.89	83.3	4.5174	0.05424
1.....	7.40	100.0	8.8450	0.08845
1.....	7.18	109.0	6.8907	0.06320
1.....	.....	110.2	3.6242	0.03290
1.....	7.66	165.6	7.9860	0.04824
1.....	7.69	169.0	12.3660	0.07314
1.....	8.58	222.0	7.2046	0.03247
1.....	9.50	329.0	14.4939	0.04403
	Females			
1.....	1.99	1.64	0.1722	0.10500
6.....	2.29	3.69	0.5178	0.14004
7.....	2.29	3.54	0.6070	0.15229
2.....	3.55	12.44	0.7584	0.06096
2.....	3.96	16.80	1.3823	0.08203
2.....	4.95	33.25	3.0339	0.09122
1.....	5.33	43.0	4.5718	0.10632
1.....	5.50	45.0	3.0414	0.06757
1.....	5.67	48.6	5.4900	0.11310
1.....	5.55	50.0	4.7042	0.09403
1.....	6.79	80.5	6.3360	0.07872
1.....	7.23	107.3	4.8515	0.04521
1.....	6.80	111.5	7.4747	0.06702
1.....	8.03	136.0	8.3100	0.06108
1.....	7.87	143.5	8.0522	0.05613
1.....	8.25	171.5	10.8664	0.06223
1.....	8.60	188.0	10.7280	0.05853
1.....	9.20	232.0	15.0788	0.06499
1.....	7.24	119.5	12.6813	0.10610†

* Weight-specific.

† Ovigerous. Not used in calculations.

If the total oxygen consumption is plotted on the body weight, the distribution is seen to be positive but nonlinear, the increase of oxygen consumption with the greater weights being less than that suggested by the trend of the smaller crabs. Placed on a relative basis by plotting the log of the oxygen consumption on the log of the body weight, the data show a high positive linear correlation (see Fig. 1). The coefficients of correlation for the sexes do not differ significantly (Fisher's z method); the combined values give an r of +0.979 with 95 per cent confidence limits of +0.958 and +0.990; that is, if many coefficients of correlation were calculated for similar samples, 95 per cent might be expected to fall between these limits. Since even the lower limit represents an extremely high correlation for biological data, it is clear that the relationship of oxygen consumption to body weight thus expressed is highly significant.

The regression of relative oxygen consumption on relative body weight derived from the correlation is of the form

$$\log O_2 = \log a + k \log W , \qquad (1)$$

or

$$O_2 = aW^k , \qquad (2)$$

in which O_2 is total oxygen consumption in cubic centimeters per hour, W is body weight in grams, and a and k are constants (the intercept and slope, respectively, of the straight line of the first equation). The values of the constants are

$$O_2 = 0.170W^{0.798}.$$

Oxygen consumption may be transformed to weight-specific oxygen-consumption rate by dividing by W; when equations (1) and (2) are thus treated, the following equations for weight-specific respiration are obtained:

$$\left.\begin{aligned}\log O_2 - \log W &= \log a + k \log W - \log W \\ &= \log a + (k-1)\log W\ ;\end{aligned}\right\} \tag{3}$$

$$\frac{O_2}{W} = aW^{k-1}. \tag{4}$$

Since k is less than 1, $k - 1$ is negative; in agreement, the log log plot of the weight-specific rate on body weight proves to be a linear negative regression (see Fig. 4). The sexes, as before, do not differ significantly, and the combined data give a correlation coefficient (r) of -0.764 with 95 per cent confidence limits of -0.574 and -0.876. This is distinctly lower than the coefficient for total oxygen consumption but still highly significant. With the insertion of the calculated values equation (4) becomes

$$\frac{O_2}{W} = 0.166W^{-0.198}.$$

These estimates differ somewhat from those obtained for total respiration, but the differences ($a = 0.170$, as compared with 0.166, and $k - 1 = 0.798 - 1 = -0.202$, as compared with $k - 1 = -0.198$) are not statistically significant. Since the correlation for total respiration is the higher, the corresponding estimates are to be preferred.

The relation of oxygen consumption to body weight in the kelp crab and the values resulting from the above equations at once suggest comparisons. Does the tissue respiration of the kelp crab, previously determined, show a similar relation to body size? Do these relations hold for other crustaceans? How do crustaceans compare with homeothermic birds and mammals for which the surface-area "law" is said to apply? These questions will be taken up in this order.

TISSUE RESPIRATION IN THE KELP CRAB

Certain constants for the respiration of the midgut gland of the kelp crab were published by Belding *et al.* (1942). The original data are here presented in Table 2. Oxygen consumption is given as Q_{O_2}, oxygen consumed in cubic millimeters per hour per milligram of dry tissue. This is, of course, a weight-specific rate and must be compared with the second type of formula given above; comparison is hindered by the fact that it is expressed on the basis of dry-tissue weight, but this does not affect the exponent. When the log Q_{O_2} is plotted on the log body weight, a negative regression is obtained, as may be seen from

TABLE 2

Q_{O_2} (CU. MM. O_2/HR./MG./DRY TISSUE) OF MIDGUT GLAND OF KELP CRAB

Males		Females			
		Nonovigerous		Ovigerous	
Body Weight (Gm.)	Q_{O_2}	Body Weight (Gm.)	Q_{O_2}	Body Weight (Gm.)	Q_{O_2}
0.50	3.04	1.70	2.75	93.0	0.82
0.76	3.08	2.40	3.98	109.0	0.47
1.15	2.10	3.30	3.07	126.0	0.85
1.90	2.87	3.95	2.29	127.0	1.26
2.00	3.21	4.50	2.91	135.0	0.66
2.50	2.86	10.1	2.13	165.0	1.35
4.10	3.80	16.0	1.78	174.0	1.33
9.20	2.70	20.0	1.79	180.0	0.77
9.50	2.39	20.5	1.80	192.0	0.73
15.70	2.14	23.0	1.87	207.0	0.60
17.80	2.38	28.0	2.27	212.0	1.05
30.7	1.77	31.0	1.39	236.0	0.91
48.4	1.57	35.0	1.27		
50.0	1.20	44.6	1.88		
52.5	1.70	48.9	2.01		
59.0	1.56	97.0	0.95		
60.0	1.79	100.0	1.28		
67.0	1.66	131.0	1.14		
70.0	1.66	142.0	1.32		
72.0	1.07	228.0	1.66		
73.0	1.08	268.0	1.46		
85.0	1.23				
88.0	1.02				
92.0	0.63				
94.0	1.51				
104.0	1.28				
162.0	1.57				
275.0	0.78				

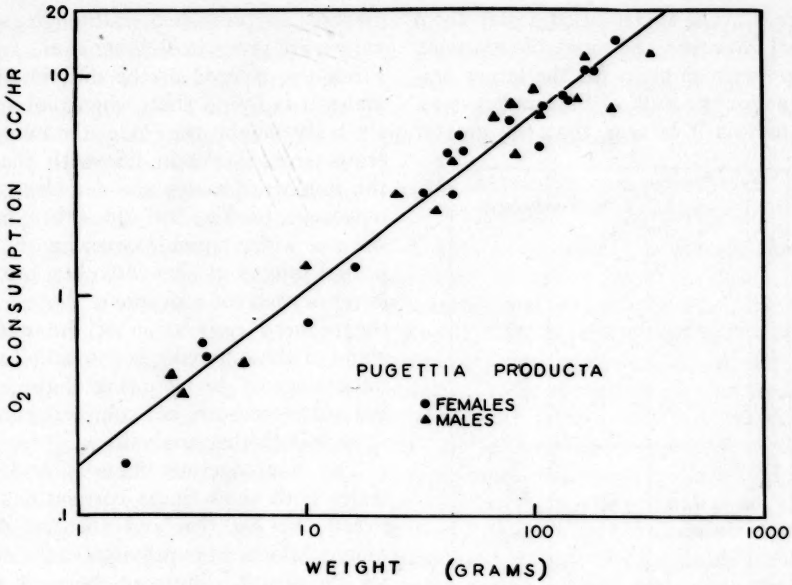

FIG. 1.—*Pugettia producta:* total oxygen consumption and body weight on double logarithmic scale. Data in Table 1.

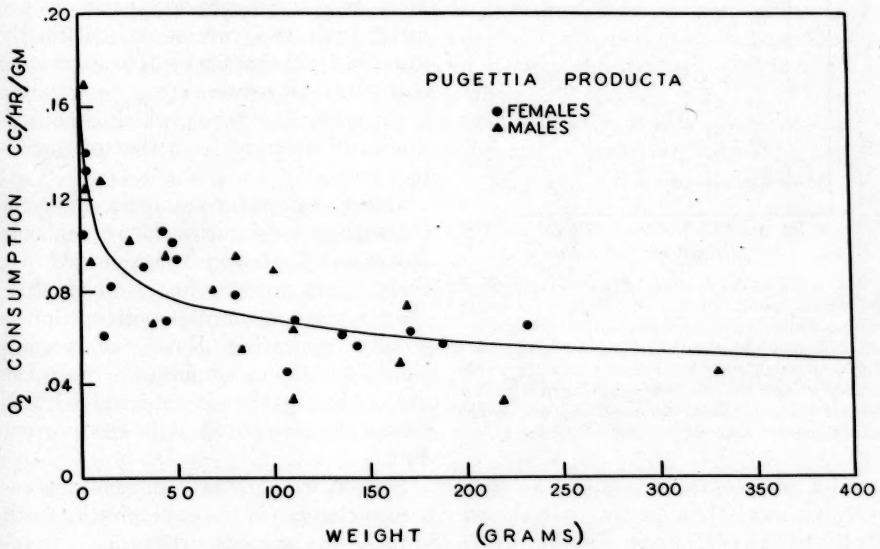

FIG. 2.—*Pugettia producta:* weight-specific oxygen consumption and body weight on arithmetic scale. Data in Table 1. The curve is from the formula $O_2/W = 0.1664/W^{0.198}$.

Figure 3. The distribution is far from normal, however, the range of Q_{O_2} being nearly twice as great for the larger animals as for the bulk of the smaller ones. On analysis it is seen that the greater

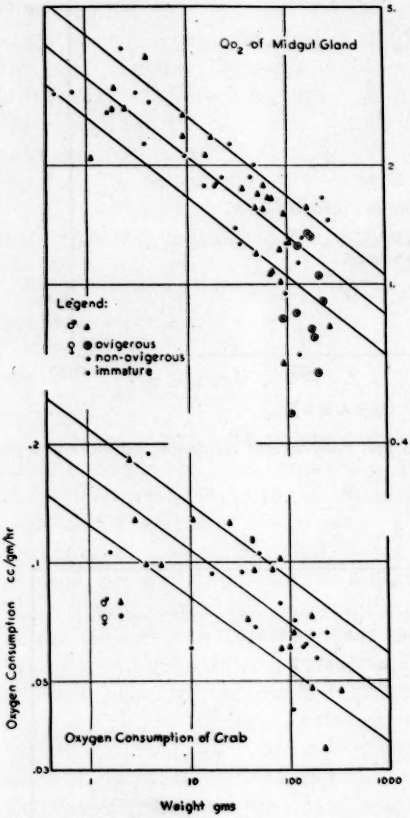

FIG. 3.—*Pugettia producta:* Q_{O_2} of midgut gland and weight-specific oxygen consumption of intact crab on double logarithmic scale. Data in Tables 3 and 1. In each plot the central line is the regression of Q_{O_2} or weight-specific oxygen-consumption rate on body weight; the two lines paralleling this lie at a distance of one standard error of estimate and should include between them 68 per cent of the cases.

variability is due wholly to animals weighing more than 65 gm. and almost wholly to females. From a study of the life-history we know that all females weighing 50 gm. or more are sexually mature (unpublished, although some values are given in Belding *et al.*, 1942). From the records of the individual females it is found that, when plotted on the body weight, the Q_{O_2} of the nonovigerous females falls in line with that of the immature males and females. The ovigerous females, on the other hand, show a wider spread, covering the expected range but also extending into far lower oxygen consumptions. Apparently the reduced respiration of the midgut gland of these females is associated with some stage of development of the eggs, but our records are not complete enough to permit further analysis.

The nonovigerous females and the males both show linear correlations between the log Q_{O_2} and the log body weight, which, as in previous cases, show no significant difference between the sexes. The correlation coefficient of the combined data, excluding the ovigerous females, is -0.820 with 95 per cent confidence limits of -0.700 and -0.895. Here, as in the weight-specific rate of the intact crab, the correlation is distinctly lower but still significant. The regression coefficient of relative Q_{O_2} on relative body weight is -0.203, which is not significantly different from that of the intact crab.

Other workers have noted a change of Q_{O_2} with age or size in various organisms. Hover and Gustafson (1926) showed that there was a decrease in the weight-specific oxygen consumption with age in the serially appearing leaves of certain plants (sorghum, sunflower). Since the size of the organism is not involved, this cannot be compared wth the present data.

Several workers have incidentally recorded changes in tissue respiration with growth in animals. Hopkins (1930) found that the respiration of clam muscle (*Venus mercenaria*) decreased with

increasing body size, and Chapheau (1932) reports a similar relation in the oyster. In neither case do the data permit analysis comparable with that of the kelp-crab midgut gland. Fox and Wingfield (1937) noted a parallelism between the total and the muscle respiration in the shrimp (*Pandalus*), but the absence of body weight prevents analysis.

Hawkins (1928) working with liver slices of the rat, Victor and Potter (1935) with lymph nodes, and Pearce (1936) with liver, heart, and kidney of the mouse showed that the Q_{O_2} decreased with increase in size; but they were interested in the variation of Q_{O_2} with age, and body weights are not given. Field, Tainter, Martin, and Belding (1937) found that the Q_{O_2} of the rabbit lens decreased with increased weight of the lens. These writers point out that, in general, the larger lenses came from larger animals but that the relation is possibly complicated by problems of diffusion.

In none of these cases was it attempted to establish the form of the mathematical relation between tissue respiration and body weight, nor does the nature of the data permit such an analysis. All, however, show that Q_{O_2} falls with increase of body size.

Determinations in some degree comparable with the present data are given by Kayser, Le Briton, and Schaeffer (1925). They measured the tissue respiration of brain and muscle (technique not given) of rats, pigeons, and fowls at two ages and chick embryos of 4, 5, 7, and 8 days, presumably entire. Body weights are given for all. The respiration of the chick embryos decreases with increase of body weight; and these data, analyzed by the methods used above, agree with our findings in other species. However, the number of cases is so small and the range of size so limited as to make the evidence of limited weight.

In spite of this evidence, impressive in the aggregate, tissue respiration is usually recorded without reference to the size of the animal from which the organ slice was obtained.

TOTAL OXYGEN CONSUMPTION IN OTHER CRUSTACEANS

A number of records of oxygen consumption in crustaceans as given by various authors are assembled in Table 3. These data are heterogeneous as to date, technique, and temperature of determination; after excluding a few as inconsistent, there remain fifty-four records, some of these redeterminations on the same animals. These were converted to the standard temperature of 15° on the basis of a Q_{10} of 1.59 obtained by calculation from records of Fox (1936) covering a reasonable range of temperatures. In spite of the fact that twenty-three species, representing more than one order, are included, the plot of the log total oxygen consumption on log body weight is linear and shows a correlation of +0.971 with 95 per cent confidence limits of +0.950 and +0.983, a highly significant relationship (see Fig. 4). These values and the constants of the regression equations are given with others in Tables 4–7 and will be discussed later.

TOTAL OXYGEN CONSUMPTION IN BIRDS AND MAMMALS

For birds and mammals the most satisfactory data on total oxygen consumption appear to be those of Benedict (1938), whose wide experience and highly developed technique assure accurate determinations. Although the number of species is not large, the values are averages of extensive experiments, and the range of body size is unusually great. Benedict, in the presentation of his data, follows the method of Kleiber (1932), with whose results he is in essential

TABLE 3

OXYGEN CONSUMPTION IN VARIOUS CRUSTACEANS

SPECIES	AUTHOR	WEIGHT (GM.)	TEMP. (° C.)	OXYGEN CONSUMPTION	
				*	†
Squilla mantis	Montuori, 1913	23.0	24.5	3.125	2.0115
	Montuori, 1913	6.5	24.5	0.769	0.4950
Callianaxa subterranea	Montuori, 1913	1.5	24.5	0.200	0.1287
	Montuori, 1913	0.65	24.5	0.089	0.0573
Carcinus moenus	Montuori, 1913	47.0	24.5	3.169	2.0398
	Montuori, 1913	34.5	24.5	2.488	1.6014
	Montuori, 1913	14.0	24.5	1.143	0.7357
	Montuori, 1913	10.6	24.5	1.216	0.7827
	Montuori, 1913	7.0	24.5	0.516	0.3321
	Montuori, 1913	1.65	24.5	0.217	0.1397
Dromia vulgaris	Montuori, 1913	102.0	24.5	6.194	3.9869
	Montuori, 1913	22.0	24.5	3.124	2.0108
Eriphia spinifrons	Montuori, 1913	96.0	24.5	5.356	3.4475
	Montuori, 1913	34.0	24.5	2.901	1.8673
	Montuori, 1913	0.45	24.5	0.262	0.1686
Galathea squamifera	Montuori, 1913	4.0	24.5	0.446	0.2871
	Montuori, 1913	2.8	24.5	0.224	0.1442
Ilia nucleus	Montuori, 1913	7.2	24.5	0.438	0.2819
	Montuori, 1913	3.5	24.5	0.350	0.2253
Maja verrucosa	Montuori, 1913	43.0	24.5	5.914	3.8066
	Montuori, 1913	4.2	24.5	0.652	0.4197
	Montuori, 1913	2.0	24.5	0.234	0.1506
Pachygrapsus marmoratus	Montuori, 1913	26.0	24.5	2.979	1.9175
	Montuori, 1913	14.6	24.5	2.886	1.8576
	Montuori, 1913	11.8	24.5	2.282	1.4688
	Montuori, 1913	8.0	24.5	0.519	0.3341
	Montuori, 1913	1.8	24.5	0.167	0.1075
Paguristes maculatus	Montuori, 1913	17.3	24.5	4.587	2.9525
	Montuori, 1913	14.0	24.5	4.040	2.6004
	Montuori, 1913	5.3	24.5	0.647	0.4165
	Montuori, 1913	4.6	24.5	0.680	0.4377
Palinurus vulgaris	Montuori, 1913	532.0	24.5	35.482	22.8386
	Montuori, 1913	75.0	24.5	4.536	2.9197
Pilumnus hirtellus	Montuori, 1913	3.6	24.5	0.440	0.2832
	Montuori, 1913	0.24	24.5	0.056	0.0360
Sicyonia sculpta	Montuori, 1913	5.3	24.5	0.837	0.5387
	Montuori, 1913	4.1	24.5	0.725	0.4667
	Montuori, 1913	2.0	24.5	0.502	0.3231
Spirontocaris cranchi	Fox, 1936	0.04	10.0	0.00574	0.0040
	Fox, 1936	0.04	17.0	0.0088	0.0080
Pandalina brevirostrus	Fox, 1936	0.15	10.0	0.0178	0.0225
	Fox, 1936	0.15	17.0	0.0200	0.0182
Spirontocaris securifrons	Fox, 1936	1.80	6.5	0.1382	0.3490
Pandalus montagui	Fox, 1936	2.20	10.0	0.2332	0.2937
	Fox, 1936	2.20	17.0	0.3122	0.2847
Astacus fluviatilis	Rogers, 1927	31.00	12.5	1.1780	1.3237
Homarus americanus	Bosworth *et al.*, 1936	189.00	15.0	6.6150	6.6150
	Bosworth *et al.*, 1936	189.00	15.0	4.7250	4.7250
	Bosworth *et al.*, 1936	189.00	15.0	3.9690	3.9690
	Bosworth *et al.*, 1936	230.00	22.0	8.5100	5.9764
Homarus?	Rogers, 1927	315.00	15.0	21.5145	21.5145
Homarus americanus	Bosworth *et al.*, 1936	324.00	22.0	12.4800	9.1692
Cancer?	Rogers, 1927	470.00	16.0	50.3840	31.6780
Palinurus?	Rogers, 1927	520.00	15.0	23.2960	23.2960

* In cubic centimeters per gram per hour at temperature cited.

† In cubic centimeters per gram per hour at 15° C. (on basis of Q_{10} of 1.59, see text).

agreement. This method consists in the calculation of ratios which correspond to a transformation of equation (2):

$$a = \frac{O_2}{W^k},$$

using a series of values for k. The value of the exponent of the weight which gave the best "constant" was found by Benedict to lie between 0.73 and 0.76. In resting state it has an enormous amount of fat. The data remaining, representing twenty-seven species, give a correlation coefficient of +0.998 with 95 per cent confidence limits of +0.996 and +0.999. The regression coefficient is +0.740, a value falling between those just quoted from Benedict (see Fig. 5). The inclusion of the elephant and the dwarf mouse would increase the exponent slightly.

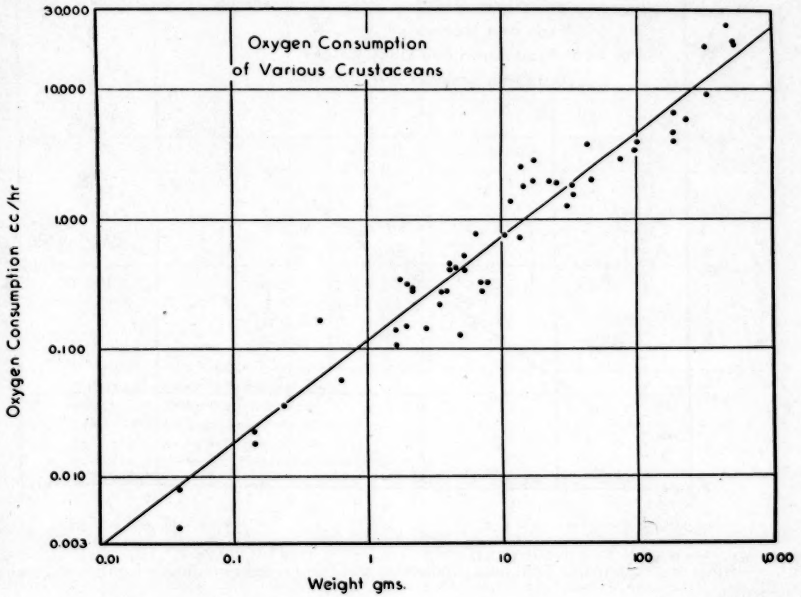

FIG. 4.—Total oxygen consumption and body weight of various crustaceans on double logarithmic scale. Data in Table 2.

calculating from his data we have omitted certain forms. These include the sow, boar, and elephant, which Benedict has also excluded from his calculations because there were too few determinations; the dwarf mouse, which cannot be considered "normal" from the point of view of endocrine function; and the marmot, which has an abnormally low metabolism—perhaps, as Benedict suggests (1938, p. 154), because in the nonhibernating state it has an enormous amount of fat. The data remaining, representing twenty-seven species, give a correlation coefficient of +0.998 with 95 per cent confidence limits of +0.996 and +0.999. The regression coefficient is +0.740, a value falling between those just quoted from Benedict (see Fig. 5). The inclusion of the elephant and the dwarf mouse would increase the exponent slightly.

There are thus available, for comparison with the data on the kelp crab, values for tissue respiration from the same species, interspecific data for other crustaceans, and determinations for a wide range of birds and mammals. This information is summarized as follows: In Table 4 are given the correlation coefficients and their confidence limits; in Table 5, the standard errors of estimate of the regressions; in Table 6, the regres-

sion coefficients of total oxygen consumption; and in Table 7, the regression coefficients of the weight-specific rates.

The close relationship represented by the present correlations (Table 4) will be better realized by comparison with a series of one hundred and forty-five correlations for man collected from the literature by Pearl (1940, p. 426). Three of the five coefficients here given exceed 0.97. Pearl lists but two having equal values. High correlations might be expected between the bones of the human skeleton; the following are the highest listed by Pearl:

Correlation between the lengths of—
First joint of forefinger of right and of left hand.....+0.925
Right ulna and of left femur.....+0.887
Right ulna and of left tibia.....+0.882
Right humerus and of right femur...+0.876

All these are below the highest three of the present work. Even our lowest coefficient, −0.764, indicates a closer relationship than that between heart weight and body weight in man. The lowest of the confidence limits of Table 4, −0.574, is exceeded by only 21 per cent of the entries in Pearl's list.

On the basis either of their absolute values or of the confidence limits, all the correlations may be considered highly significant. This point is emphasized since it is one of the clearest arguments for the validity of the type of equation here used, often called the "power relationship." No other reasonably simple expression for the relation of oxygen consumption to body weight has been proposed which shows as high a correlation.

The correlation coefficients fall readily into two groups, one of 0.97 or above, the 95 per cent confidence limits of which do not fall below 0.95, and a second of 0.82 or less, with confidence limits which do not exceed 0.90. The first in-

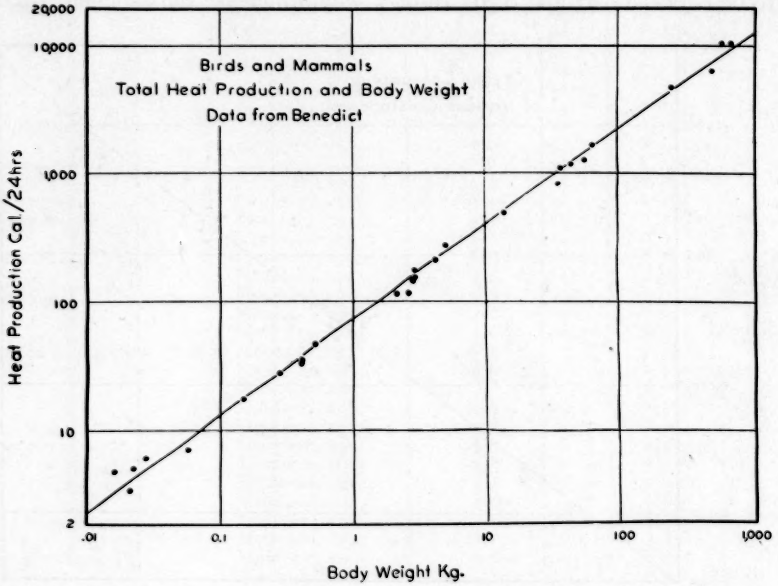

FIG. 5.—Birds and mammals: total heat production and body weight on double logarithmic scale. Data from Benedict.

cludes all of the relations of total oxygen consumption to body weight; the second, the weight-specific oxygen rates. This difference in the values of the coefficients results in part from the nature of the correlations. The total oxygen consumption and the body weight represent two independent determinations; the weight-specific rate represents a ratio between oxygen consumption and body weight; the body weight with which it is correlated has already entered into this ratio. As a result, a correlation will be introduced even when the total oxygen consumption and weight showed none. This so-called "spurious correlation" is well known to statisticians. For instance, if we make the extreme assumption that there is no correlation between respiration and size, so that the oxygen consumption of all animals of whatever size is the same, and calculate a series of weight-specific oxygen rates by dividing this constant oxygen consumption by the body weight, the rates will, of course, decline with increase in the size of the animal. If, now, the rates are correlated with the body size, a negative coefficient will result although the original values were independent. If, as is here the case, there is a positive correlation between the original values, the resulting negative correlation of the weight-specific rates will be lowered. Although the weight-specific rate is very useful for comparisons and is at times the only measure possible, as in the case of tissue respiration, its relationship to weight or other factors must always be interpreted with caution.

TABLE 4

CORRELATION COEFFICIENTS

	Mammals*	Kelp Crab Total†	Various Crustaceans‡	Qo_2§	Kelp Crab Wt.-Sp.‖
Number	27	34	54	49	34
r	0.998	0.979	0.971	− 0.820	− 0.764
r_1¶	0.996	0.958	0.950	− 0.700	− 0.574
r_2¶	0.999	0.990	0.983	− 0.895	− 0.876
k	0.063	0.202	0.239	0.572	0.645
$100r/r+k$	94.04	82.88	80.24	58.89	54.21
$100k/r+k$	5.96	17.12	19.76	41.11	45.78
r^2	0.996	0.959	0.943	0.672	0.584
k^2	0.004	0.041	0.057	0.328	0.416

* Mammals and birds, Benedict's data.
† Kelp crab, total oxygen consumption.
‡ Various crustaceans, data from literature.
§ Qo_2 of the kelp-crab midgut gland.
‖ Weight-specific respiration rate of kelp crab.
¶ r_1 and r_2 are the lower and upper limits of the 95 per cent confidence limits of r.

If, on the other hand, we compare the standard errors of estimate, showing the extent of the scatter about the regression of oxygen on body weight, we find that, in part because of the lesser absolute range, the weight-specific rates appear in a rather more favorable light. Since the data are in logarithmic form, the standard error of estimate must be expressed as a percentage of the estimated value of oxygen consumption. (Mills [1924, p. 457] discusses the interpretation of the standard error of estimate when this is expressed in logarithmic form. See also Schrek, 1942.) From Table 5 it will be seen that 95 per cent of the weight-specific oxygen-consumption records may be expected not to differ by more than

about 8 per cent from the values represented by the regression line. On the other hand, in the regression of total oxygen consumption on body weight in the kelp crab, a variation of approximately 25 per cent is required to include 95 per cent of the values, and other data are still more variable.

In Table 6 are given the regression coefficients, k, of total oxygen consumption on body weight, the differences arising from intercomparisons, and the significance of these differences.[1] An analysis of the table leads to the following three conclusions:

a) The kelp crab and the group of

TABLE 5

STANDARD ERROR OF ESTIMATE

	No.	r	$S_{y \cdot x}$ (log)	95 PER CENT CONFIDENCE LIMITS IN PERCENTAGES	
				Upper	Lower
Kelp crab (weight-specific rate)	33	−0.764	0.0178	8.4	7.7
Q_{O_2} (kelp-crab midgut gland)	48	−0.820	0.0180	8.5	7.8
Mammals (weight-specific rate)	27	−0.946	0.0465	23.4	18.9
Kelp crab (total respiration)	33	+0.979	0.0555	28.5	22.2
Mammals (total respiration)	27	+0.998	0.0745	40.0	28.5
Various crustaceans (total respiration)	53	+0.971	0.1870	132.5	57.0

TABLE 6*

COMPARISON OF REGRESSION COEFFICIENTS (k) FOR TOTAL RESPIRATION

No.	Form	k	Surface-Area "Law" (0.667)	Mammals (0.740)	Kelp Crab (0.798)
54	Various crustaceans	0.826	0.159	0.086	0.028
			5.29	4.77	1.22
			0.001	0.001	0.2
34	Kelp crab	0.798	0.131	0.058	0.000
			4.47	5.03	.....
			0.001	0.001	.....
27	Mammals	0.740	0.073	0.000	.....
			7.44	.....	.....
			0.001	.....	.....

* The three values in each cell represent, from above downward, the difference in k, the t value, and P, the probability of the occurrence of this difference by chance.

[1] Since the methods of comparing regression coefficients are varied and not always clearly stated, the formula used is given below in detail. The method is essentially that of Fisher (1936, 6th ed., sec. 26, p. 137, and sec 26.1, p. 146) but follows the arrangement of Simpson and Roe (1939, p. 278) with certain modifications introduced by Rider (1939, p. 93).

$$t = \frac{k_1 - k_2 \, (\Sigma X_1^2 - N_1 \bar{x}_1^2) + (\Sigma X_2^2 - N_2 \bar{x}_2^2) \, (N_1 + N_2 - 4)}{\sqrt{\Sigma Y_1^2 - N_1 \bar{y}_1^2 (1 - r_1^2) \frac{N_1 - 1}{N_1 - 2} + \Sigma Y_2^2 - N_2 \bar{y}_2^2 (1 - r_2^2) \frac{N_2 - 1}{N_2 - 2}}}.$$

various crustaceans do not differ significantly in the value of the coefficient k. It should be noted that in the case of the kelp crab the relationship is intraspecific, the records coming from individuals of the same species differing both in size and in maturity, while in the other group it is interspecific, being derived chiefly from mature individuals of different species. It may safely be concluded that the experimental results obtained on the kelp crab are typical of the higher crustacea.

b) The regression coefficients of both sets of crustacean data differ significantly from that of mammalian data. Although significant, the differences are not great, the crustacean coefficients exceeding that of the mammals by 7.8 and 11.6 per cent, as compared with a 3.5 per cent difference between the crustacean coefficients. That there are greater differences between the crustaceans and the mammals than among the crustaceans is not surprising. It seems probable that the similarities among the animals here considered are more significant than their differences.

c) Both crustaceans and mammals show coefficients (k) significantly higher than the two-thirds required by the surface-area "law," these differences ranging from 11 to 24 per cent. This is a point of particular importance since it is critical in deciding between the merits of the proposed method of treatment and those of its nearest rival. The surface-specific rate—for example, kilocalories per square meter—is in general use because it more nearly deserves the name of "constant" than does the weight-specific or other rates previously proposed.

It should be noted, however, that actual surface areas have seldom been used, or indeed determined. What is called "surface area" is a mathematical fiction based on the weight. For animals this is given by the Meeh formula,

$$S = kW^{2/3},$$

where S is the surface area, W is the weight, and k a constant to be determined for the particular species and the units used. For man, more elaborate expressions have usually been employed, of which that proposed by Du Bois is the best known:

$$S = W^{0.425} H^{0.725} k,$$

in which H is the height and k a constant. This is not as different from the Meeh formula as would at first appear. If the exponents are combined on the assumption that H is proportional to $\sqrt[3]{W}$, or $W^{0.333}$, then

$$(W^{0.333})^{0.725} = W^{0.241}$$

and

$$W^{0.425} \times W^{0.241} = W^{0.666} = W^{2/3}.$$

Although there is a decreasing tendency among workers to look upon the relation between surface area and oxygen consumption as a "law" and a growing tendency to regard it as a convenience, the surface-specific rate is in almost universal use. Both Kleiber (1932) and Brody and Procter (1932) have pointed out what the above data show, that the surface-specific rate varies more than one based on some power of the weight between 0.70 and 0.80. It is a readily understandable mathematical fact that an exponent derived from the data would fit these data better than an arbitrary one supported by little beyond custom. Certainly in all of the present data the "best" fit is given by values significantly different from 0.666.

Turning to the intercomparisons of the weight-specific rates (Table 7), we find that rather more data are available. These include regression coefficients for the kelp crab, for the Q_{O_2} of the kelp-

crab midgut gland, and for mammals; for these there are available measures of variability from which the significance of the differences can be calculated. These may also be satisfactorily compared with a theoretical value, such as −0.333, derived from the surface-area "law" (0.666 − 1 = −0.333). In Table 7 are included, for convenience, some values calculated, as above, from the regression of total oxygen consumption; these have no measure of reliability but have been compared roughly as if they represented theoretical values. Since the probabilities are all very small, the comparisons are undoubtedly significant.

Keeping in mind these different criteria of significance, we may list the conclusions to be drawn from Table 7.

a) The crustacean data are homeogeneous. There are no significant differences between the weight-specific rate for the kelp crab and that calculated from the total respiration of this animal or from the other group of crustaceans. Likewise the regression coefficient of the QO_2 of the midgut gland on the body weight is not significantly different from that derived from the respiration of the entire animal.

TABLE 7*

COMPARISON OF REGRESSION COEFFICIENTS ($k - 1$) FOR WEIGHT-SPECIFIC RESPIRATION

	No.		($k-1$)	7 −0.333	6 −0.260	5 −0.250	4 −0.203	3 −0.202	2 −0.198
1.....	54	Various crustaceans	−0.174	0.159	0.086	0.076	0.029 1.36 0.2	0.028	0.024 0.801 0.4
2.....	34	Kelp crab (weight-specific rate)	−0.198	0.135 4.51 0.001	0.062	0.052 3.44 0.001	0.005 0.346 0.7	0.004 0.134 0.9	0.000 ....
3.....	34	Kelp crab (from total)	−0.202	0.131	0.058	0.048	0.001 0.047 0.9	0.000	....
4.....	49	QO_2 midgut gland	−0.203	0.130 6.11 0.001	0.057	0.047 3.70 0.001	0.000	....	....
5.....	27	Mammals (weight-specific rate)	−0.250	0.083 4.76 0.001	0.010 0.574 0.6	0.000	....	....	....
6.....	27	Mammals (from total)	−0.260	0.073	0.000	....	....	....	....
7.....	.....	Surface-area "law"	−0.333	0.000	.....	.....	.....	.....	.....

* The three values in each cell represent, from above downward, the difference in k, the t value, and P, the probability of the occurrence of this difference by chance. In some cases where the comparison has little meaning or the data for judging the statistical significance is lacking, only the difference is given.

b) In a similar manner the mammalian data are homogeneous.

c) The crustacean and the mammalian data show coefficients significantly but not widely different (23 and 26 per cent).

d) The regression coefficients of both the crustacean and the mammalian data are significantly and widely different from the −0.333 required by the weight-specific form of the surface-area "law" (33 and 68 per cent).

These conclusions support in detail

those drawn from the comparison of the regression coefficients of total oxygen consumption on body weight.

INTENSITY OF RESPIRATION

Two general questions require further consideration—that of the intensity of respiration and the units in which it should be measured and that of the regulation of respiration. When it is asked at what size or in what species respiration is most intense, several questions are combined, and their separation and analysis must precede any clear answer. What is meant by "intense"? To most chemists and many biologists it suggests activity per unit of weight; if this is accepted as a definition, a statement of the weight-specific rate of respiration—for example, in cubic centimeters of oxygen consumed per hour per gram body weight—is the proper answer. To some physiologists "intensity" will suggest activity per unit area. For this smaller group who accept a definition in terms of area, a surface-specific rate will be the proper answer.

If it is objected that the weight-specific or the surface-specific rate is not constant, it merely underlines the fact that by either of these definitions the intensity of respiration declines with increasing size. What, then, is the use of a constant if such can be found? The problem is the statistical one of partial correlation. In the present case we are considering oxygen consumption which is known or believed to vary with a number of factors, including species, body weight, age, sex, surface area, climate, diet, and various diseases. If any one of these relations can be determined and allowed for, the others may be more readily analyzed. If, for example, we can determine the correlation between oxygen consumption and body weight, we are in a position to study the relation of respiration to sex, "weight being held constant"; that is, we may obtain the partial correlation of oxygen consumption and sex.

The data of metabolism are variable, owing both to individual variability and to the errors of technique; the effect on respiration of many of the factors is perhaps small and difficult to see against this background of variability; in consequence, adequate data for useful partial correlations are not yet available.

The high correlation between relative oxygen consumption and relative body weight, however, indicates that it is possible largely to eliminate the factor of size. The general formula may be written

$$a = \frac{O_2}{W^k},$$

and the constant a may be taken as indicative of metabolism when the influence of body weight is canceled out. Thus, if animals differing in size and sex are compared, the value of a will show some random variation from individual to individual; but a systematic difference must result from sex. In this manner the influence of minor factors, commonly obscured by the dominant effect of size, may be brought to light.

The extent to which body weight dominates the variability of oxygen consumption is indicated by the correlations of Table 4. The correlation of total oxygen consumption with body weight in the kelp crab may serve as an example (the total oxygen consumption is chosen to avoid the spurious correlation involved in weight-specific rates). Here $r = 0.979$, $r^2 = 0.959$, $k = 0.202$, and $k^2 = 0.041$. Variation may be expressed either in terms of variance (S_x^2) or of standard deviation (S_x). From the value of r^2 it is apparent that 96 per cent of the variance in oxygen consumption is associated with variance in body weight and only 4 per

cent with the variance in all other factors. Since the sum of r and k exceeds unity, we cannot interpret r in terms of per cent; but 83 per cent of the standard deviation of oxygen consumption is associated with variation in size ($100r/r + k$), and 17 per cent ($100k/r + k$) is associated with other factors. For the total oxygen consumption of the crustaceans in the literature the relation is slightly less close ($r = 0.971$); for mammals, much closer ($r = 0.998$).

These values strikingly illustrate the importance of body size as a factor in oxygen consumption and the hopelessness of analyzing other factors unless size is eliminated by expressing oxygen consumption as an involute weight–specific rate (Q_{W^k}) or by some similar device.

What is the significance of a? It is the quotient of an oxygen consumption divided by a power of the weight and so may be called an "involute weight-specific rate." In place of the symbol a, often used with other meanings, the expression Q_{W^k} is proposed with the suggestion that, when used in a particular case for which the value of k has been calculated or assumed from other sources, this value be inserted. Thus for mammals, if Benedict's data are used, it would become $Q_{W^{0.74}}$. As to units, it is urged that respiration be expressed in terms of oxygen consumption rather than heat production, unless the heat production has actually been measured or the value of the respiratory quotient is known, so that the transformation of oxygen to kilocalories may have real significance. In the interests of uniformity it is suggested that oxygen be stated in cubic centimeters at normal pressure and temperature, body weight in grams, and time in hours. The symbol Q_{W^k} would thus indicate the number of cubic centimeters of oxygen consumed per hour per gram body weight to the kth power.

A more concrete meaning is furnished by the following: Since $W^k = 1$ when $W = 1$, Q_{W^k} represents the oxygen consumed by an animal weighing 1 gm. If animals of 1 gm. weight are possible, this is a straightforward statement; but for horses or dogs it must be interpreted as meaning "if animals weighing 1 gm. existed and the observed relation between oxygen consumption and body weight was found to extend to them."

It will be clear from the above discussion and literature previously cited that Q_{W^k} applies to tissue as well as total respiration. It will also be clear that, while k will be unaffected, the absolute value of Q_{W^k} for total and for tissue respiration will not be the same unless both have been calculated on a wet-weight basis. To facilitate comparisons involving total and tissue respiration, we recommend that tissue respiration be calculated on a wet basis and that the value of Q_{W^k} be given as well as more customary measures, such as Q_{O_2}. While it is generally recognized that the weight-specific rate varies with body size, it is almost universal to give values of Q_{O_2} without any indication of the weight of the animal from which the tissue was obtained. It is as necessary in tissue as in total respiration to eliminate the effect of body weight by using Q_{W^k}.

Prepared on this basis, Table 8, presenting the values of Q_{W^k}, permits the comparison of data for the various groups of animals considered in the present paper. The group of crustaceans represented in the literature falls below the "intensity" of respiration of the kelp crab. This probably results from the conversion to 15° by a Q_{10} not based on the majority of the species concerned and apparently too low.

The Q_{W^k} of the midgut gland is about six times that of the animal from which the tissue is derived. This is reasonable,

since the midgut gland is one of the more active tissues and there is a large proportion of shell with a low respiration in the intact crab. The Q_{W^k} of the midgut gland at 15° is about one-third of that of the whole mammal at 37°. Compared with the various rat tissues on the same basis, the Q_{W^k} of the midgut gland corresponds to the less active tissues, with a value slightly below that of the skin and above that of the skeleton, ligaments, and the tal muscle, skin, and the less active tissues. The general features of the comparison are about what might be expected; at its habitual temperature the crab has a respiration less than one-tenth that of a mammal, while its perhaps most active tissue exceeds a few of the less active tissues of the mammal. If transformed to the temperature of the mammal, the respiration of the crab is nearly one-third that of the mammal.

TABLE 8

VALUES OF Q_{W^k}

	Cc./Hr./Gm. 15° C.		Cal./Day/Kg.			
			15° C.		37° C.	
	Q_{W^k}	Per Cent	Q_{W^k}	Per Cent	Q_{W^k}	Per Cent
Mammals:						
Benedict				100	72.7	100
Kleiber					70.5*	
Brody					73.3*	
Crustaceans:						
Kelp crab	0.170	100	4.84	6.7	22.2	30.5
Various	0.108	64	3.73		17.1	
Tissue:						
Midgut gland wet	0.995	586	28.3	38.9	129.8	178.5
Midgut gland dry	3.379		96.0		441.0	

* Approximate.

blood (Field, Belding, and Martin, 1939). These comparisons are made at temperatures differing by 22°, but to reduce them to the same temperature requires assumptions that are hardly justified. Neither the crab nor its midgut gland will survive at 37°; the mammal will usually not survive a body temperature of 15°, although its tissues will. For this hardly biological comparison the Q_{W^k} of the midgut gland has been converted to a temperature of 37° on the basis of a Q_{10} of 2.00 (cf. Belding *et al.*, 1942, p. 87). The value is now below that of the rat kidney, brain, liver, heart, and diaphragm and above that of skele-

REGULATION OF RESPIRATION

The present finding, that the exponent k of the equation

$$O_2 = aW^k$$

for the kelp crab agrees within the limits of accuracy of the data with the corresponding exponent for one of its tissues, the midgut gland, supports the recent statement of Weymouth, Field, and Kleiber (1942) that the exponents of total and of liver respiration in rats, rabbits, and sheep are the same. If total and tissue respiration bear the same relation to body weight in animals as diverse as mammals and crustaceans, it irresistibly

suggests some mechanism by which respiration is regulated. What would such a mechanism have to account for? The respiration of an animal is the sum of the respiration of its component tissues. The regressions of the weight-specific rates for the different tissues apparently form, in the log log plot, a family of parallel lines, some higher and some lower, corresponding to the intensity of respiration in the particular tissue, but all showing the same slope as the regression of the weight-specific rate of the entire animal. Animals of varying sizes in one species (intraspecific comparison) show a relation of respiration to body weight very similar to (but probably differing in detail from) that of adults of various species (interspecific comparison) (cf. Brody and Procter, 1932).

What mechanism can account for this relatively simple but pervasive relation? The regulation is not a function of body surface, since in all cases the exponent is significantly different from the value of two-thirds required by the surface-area "law." Heat loss is not essentially involved in the regulation. The completely heterothermic crab shows the same relation between resting oxygen consumption and body size as do representatives of the only two groups that regulate body temperature—birds and mammals. The regulation is not systemic, through control of the blood flow, oxygen supply, muscle tone, or the like, since it is operative during the period of survival of excised organ slices in an atmosphere of pure oxygen. Although data are not at hand to establish the point, we are inclined to think that the primary regulation is through genetic control of the development of intracellular enzymes.

The relation here seen between respiration and body weight may be expressed by the same formula used by Huxley and Teissier (1936; see also Huxley, 1932) in analyzing relative or heterogonic growth. Parts such as the chelae of crabs and the heart of mammals bear to the whole a relation written by Huxley and Teissier as

$$y = bx^{a}.$$

This formula applies equally to the chemical constituents of the organism. This aspect has been less studied than that of parts and organs, but fairly diversified examples are available. Huxley (1932, p. 29), Brody, Procter, and Ashworth (1934), and particularly Needham (1934) may be cited. Needham has assembled records for seventeen substances, the relation of which to total weight may be expressed by the power formula, applicable either to relative growth or, as in this paper, to oxygen consumption. Some of the values for the exponent k fall in the range given above for respiration. It is therefore not unreasonable to assume that the concentration of respiratory enzymes in a particular type of cell may develop as do other chemical constituents and, with the attainment of full statute, show a relation to body weight which may be expressed by the power formula.[2] The exponent of 0.74 which we have seen in the relation of respiration to body weight in adult mammals may therefore result from the "relative growth" of the respiratory enzymes in the individual cells.

[2] This hypothesis is strongly supported by evidence appearing while this paper was in press. Rosenthal and Drabkin ("The Cytochrome *c* Content of Normal and Neoplastic Mammalian Epithelium, and Its Correlation with Body Mass, *Jour. Biol. Chem.*, **150** (1943): 131–41 give the cytochrome *c* concentration of the kidney cortex and the body weight of the mouse, rat, rabbit, dog, pig, man, and horse. The regression coefficient of the log cytochrome *c* concentration on the log body weight for this data is −0.278, a value apparently not significantly different from that of the weight-specific oxygen-consumption rate of the series of mammals treated above. One of the known respiratory enzymes is thus found in the concentrations predicted.

Obviously, this does not "explain" the regulation of respiration, but it does show that the relation of the concentration of the respiratory enzymes to the body weight is not unique but merely a particular case of the general relation exhibited alike by organs, parts, and chemical constituents of animals.

SUMMARY

1. The oxygen consumption of the kelp crab, *Pugettia producta* (sixteen males and eighteen females, ranging in weight from 1.64 to 329 gm.), was studied by a constant-flow method. Since oxygen consumption was found to be reduced by partial pressures below 70 mm. Hg, all determinations were made at or above 100 mm.

2. The total and the weight-specific oxygen consumption of the intact crab and the tissue respiration (Q_{O_2}) of the crab midgut gland (previously determined) have been analyzed and compared with the oxygen consumption recorded for other crustaceans and the equivalent heat production of birds and mammals. The following relations were found:

a) For the present crab data there is no significant difference in oxygen consumption between the sexes.

b) Intraspecifically (present data) and interspecifically (data from the literature) oxygen consumption in crustaceans increases with increasing body weight, showing a relation qualitatively similar to that observed in birds and mammals. The relative oxygen consumption increases at a constant rate with increase of relative body weight, so that on logarithmic co-ordinates the regression of oxygen consumption is a straight line with a positive slope, or oxygen consumption varies with body weight according to the "power law." This relation may be expressed by the following formulas:

$$\log O_2 = \log a + k \log W ,$$
$$O_2 = aW^k ,$$
$$a = \frac{O_2}{W^k} ,$$

where O_2 is oxygen consumption, W body weight, a and k constants (the intercept and the slope, respectively, of the regression line).

c) Similarly, the relative weight-specific oxygen-consumption rate of the crab and the tissue respiration of the crab midgut gland, and the weight-specific oxygen-consumption or heat-production rates of birds and mammals all fall with increasing body weight. The general regression formula is as follows:

$$\frac{O_2}{W} = aW^{k-1};$$

or, since k is less than 1 and $k - 1$ therefore negative,

$$\frac{O_2}{W} = \frac{a}{W^{k-1}} ,$$
$$a = \frac{O_2}{W} W^{k-1} .$$

3. Oxygen consumption varies with many factors, among which body weight plays a dominant role. The correlation between total oxygen consumption and body weight is high, ranging from 0.971 to 0.998; the relation between weight-specific oxygen consumption and body weight has been avoided because of the spurious correlation involved. For the kelp crab, 96 per cent of the variance and 83 per cent of the standard deviation is associated with body weight, and only 4 per cent of the variance or 17 per cent of the standard deviation is associated with all other factors. Since the elimination of the variability caused by weight throws into relief the effect of other factors, it is suggested that results of total, weight-specific, or tissue respiration be

expressed as *involute weight-specific* rates, corresponding to the a of the above formulas, for which the more distinctive symbol Q_{W^1} is proposed.

4. If Q_{W^1}, the involute weight-specific rate, is accepted as a measure of the *intensity* of respiration and the animals are considered at their "habitual" temperatures (37° C for the mammal and 15° C. for the crab), the respiration of the crab is about one-fifteenth that of the mammal. The intensity of the respiration of the midgut gland is about six times that of the entire animal and about equal to that of the less active tissues of the rat, such as the skin and skeleton.

5. It seems necessary to postulate a widespread mechanism of metabolic regulation assuring that the relative intra- and interspecific total oxygen consumption, relative weight-specific respiration rate, and the relative rate of tissue respiration maintain a simple relation to relative body weight. This regulation is not a function of body surface, since in all cases the exponent is significantly different from the two-thirds required by the surface-area "law." Heat loss is not essentially involved, since the heterothermic crab shows the same relation as do representatives of the only groups in which temperature is regulated—birds and mammals. The regulation is not systemic, through control of the oxygen supply, muscle tone, or the like, since it is operative during the period of survival of excised tissue slices in an atmosphere of pure oxygen. The most probable mechanism would appear to be that regulating the development of intracellular enzymes, the concentrations of which, as of other chemical constituents of the organism, appear to maintain during the growth and maturity of the cell a power relation to the total weight of the cell.

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PHYSIOLOGY OF THE SILKWORM

I. GROWTH AND RESPIRATION OF BOMBYX MORI DURING ITS ENTIRE LIFE-CYCLE

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I

THE economic importance of the domestic silkworm, *Bombyx mori*, has rendered the cultivation of this insect a well-established art in many parts of the world. Through centuries of practice numerous strains of the insect have been established, and the procedure for their culture has become standardized. As an experimental material, the silkworm deserves a place in the biological laboratory comparable to the fruit fly, the white rat, and certain microörganisms. Aside from possessing desirable traits as experimental material, the silkworm is suited for the study of a number of problems in general and insect physiology, as well as in biochemistry. In transforming the foodstuffs obtained from the leaves of the mulberry plant into the protein of the silk secreted during the spinning of the cocoon, the silkworm performs a process which has so far defied the chemist to duplicate in his test tube (Shelton and Johnson, 1930). The chemical events and the mechanism of metamorphosis, including the mechanism of molting of insects in general, still re-

main among the little-understood problems in insect physiology (Wigglesworth, 1939), and the study of the developing eggs of the insects affords a suitable approach to the understanding of the metabolism during embryonic development in general (Needham, 1931, and Bodine and associates in a series of papers starting in 1934).

In this account and in the articles to follow, we propose to use the domestic silkworm as material for the study of the chemical events taking place during the metamorphosis of this insect, with special emphasis on the mechanism of silk formation. The present account presents data for the growth and respiration obtained simultaneously on a single strain of silkworm during its entire life-cycle—from the egg stage of one generation to the egg stage of the next. Such data, of interest in many ways, appear to be lacking in the literature.

II

The variety of silkworm used in these experiments, known as Yellow Skin (YS) from the coloration on its body, was obtained from the Yunnan Sericulture Station. It is a pure strain of univoltine insect which, if properly cared for, hatches on the eleventh to the twelfth day after being taken out of cold storage. The larval period lasts for 36 days, of which 8 are spent in the first instar, 5 in the second and third instars, 4 in the fourth, and 8 in the fifth instar. Molting occurs at the end of each instar, lasting for 24–36 hours; the longer period is for the third and fourth molts. The fifth molt occurs in the cocoon, 2–3 days after completion of spinning. Spinning takes place on the ninth day of the fifth instar, with the cessation of feeding; and the process lasts for 3 days. The mature moth emerges from the cocoon in 15–21 days, the exact period depending on environmental conditions. When fertilized immediately after emerging, the female lays its eggs in a few hours, after which both the male and female die in a few days. If unfertilized, the female may also lay eggs; but in that case they are not fertile, and the rate of respiration is low. The fertilized eggs of this race of silkworm will enter into their rest period and will not develop until after winter—a lapse of about 9 months. But, when properly treated immediately after laying—with dilute HCl, for instance—the eggs may develop without entering into diapause, and will hatch in about 12 days in a suitable environment.

Feeding takes place only during the larval period, ceasing during each molt, and is heaviest in the middle of each instar. It is during the larval period that growth in weight takes place, and the final weight is of the order of many thousand times the initial.

The change in weight in the silkworms was followed throughout its life-cycle by daily weighings of the eggs, of the larvae, and of the pupae. For the eggs, a batch of 600 was weighed from day to day. For the larvae, this procedure is impracticable, and different batches were weighed from day to day. The number of larvae in each batch varies from 50 in the first two instars to 10 in the remaining instars. As far as possible, the weight of the same batch of 10 pupae was followed daily; but, because of death, substitution with fresh pupae had to be made during the period of pupation. The weights of the matured moths were obtained before and after fertilization and, for the female, also after the laying of the eggs.

The temperature at which the silkworms were kept was maintained at 24°–27° C. throughout the experiment, which lasted for 65 days. Respiration was followed daily for a period of 20 minutes, and sometimes longer, depending on the

intensity of respiration. Warburg micro-respirometers were used, with the usual conical vessels of about 15 ml. capacity. The eggs, larvae, or pupae were placed in the main vessel, with 0.2 ml. of 10 per cent NaOH in the inset for a time, to obtain the rate of O_2 consumption. The alkali was replaced with a like amount of 10 per cent HCl after the O_2 consumption measurement was made, so that the difference in CO_2 production and O_2 consumption was obtained on the same lot of organisms for the respiration-quotient (R.Q.) measurement. The respirometers were placed in a thermostat maintained at 24°, without shaking. For the experiments with eggs, 600 eggs were placed in each vessel for the duration of 10–12 days until they hatched. In the case of the pupae, this method was followed, as far as possible, with only one in each vessel; but, owing to deaths, replacements with fresh pupae had to be made during the course of the experiment. This procedure could not be followed in experiments with larvae, where a fresh batch of material had to be used each day and where the number of individuals in each batch varied from 50 in the first two instars to 3, 2, and finally 1, in the later instars.

III

For the race of silkworm (YS) used, at 24° the hourly rate of O_2 consumption in cubic millimeters per individual (Q) is 0.0187 for the unfertilized and 0.056 for the just-laid fertilized eggs. As the fertilized eggs enter into their resting period, the rate decreases to 0.0437 in 24 hours; and after a month's time, to 0.005. These values, when expressed in terms of cu. mm. per milligram of fresh weight per hour (Q') are, for the unfertilized eggs, 0.0392 cu. mm. and, for the fertilized eggs, in the order named above, 0.113, 0.092, and 0.01. Thus the fertilized eggs respire three times as fast as the unfertilized ones immediately after hatching, but during diapause the rate falls to a very low level.

The low rate of respiration in the diapause eggs may be compared with the eggs of the previous year. The value of Q' for these eggs 7 days after being taken out of cold storage is 0.38, which is about four times faster than the just-laid eggs and almost forty times faster than the month-old diapause eggs. For the eggs activated with HCl the respiration on the first day after being taken out of cold storage is 0.21, which is twenty times that for the diapause eggs and twice that for the just-laid fertilized eggs. From this initial value of 0.21, the Q' for the acid-activated eggs rises in an acclerating manner, so that it is 0.406 on the seventh day and 0.72 on the tenth, the day before hatching. The last two values are of the same order of magnitude as those for the normally developing eggs, taken out of cold storage, in which they were kept over winter, and not treated with acid. The values of R.Q. for the developing eggs are 0.79 on the first day of incubation, 0.9 on the second, 0.75 on the third to the fifth days, 0.8 on the sixth day, and 0.7 on the seventh day. A minimum value of 0.64 occurs on the eigth day of incubation, after which R.Q. rises to 0.72 and 0.75 on the last 2 days before hatching. The weight of the eggs, as was to be expected, decreased steadily from 0.49 mg. per egg to 0.46 mg. per egg from the first to the last day of incubation. These relations are given in Figure 1.

The increase in the body weight of the larvae, as was to be expected from the growth curves of other insects and higher organisms, follows a series of five S-shaped curves, the duration of which varies from 8 days for the first and fifth instars, to 5 days for the second and third instars, and to 4 days for the fourth instar. For this race of silkworm, under the condi-

tions employed in our experiments, the larval life lasted for a total of 36 days, not including the 3 days for spinning. During this interval the weight of the larvae increased from 0.35 mg. on the first day to 2,418 mg. on the last day of feeding, just before spinning—an increase of seven thousand times. The rate of O_2 consumption, expressed in cubic millimeters per individual (Q), follows the course of the growth curve very closely; but the values of Q' vary from a maximum of 2.95 cu. mm. per milligram on the first day of the larval life to a minimum of 0.32 cu. mm. on the first day of spinning. The values at the first, second, third, and fourth molts and on the last day of feeding are, respectively, 1.2, 0.94, 0.84, 0.82, and 0.75.

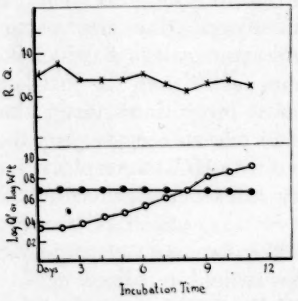

FIG. 1.—The weight in logarithm milligrams per egg (●), log Q' (cubic millimeters of O_2 consumed per egg per hour) (o), and R.Q. (×) of silkworm eggs plotted against time in days after being taken out of cold storage. Eggs hatched on eleventh day.

The rate of O_2 consumption, when expressed in terms of cubic millimeters of O_2 consumed per two-thirds power of body weight (Q''), which is equivalent to expressing the rate in terms of body surface, shows a certain degree of regularity. These values are plotted in Figure 2, together with the curve for body-weight data. There appears to be a "basal" rate of O_2 consumption which is maintained throughout the larval life, rising slightly with age, and this "basal" rate is disturbed through feeding and activity during each instar. Thus, during the first instar the initial value of Q'' is 1.75, which is only slightly increased during the feeding period. There is a considerable rise in Q'' associated with feeding and activity in the middle of the second instar, declining to the "basal" value of 2.17 at the second molt, after which there occurs another rise associated with feeding and activity during the second instar. The value of Q'' at the third molt is 3.5; that at the fourth molt and on the first day of spinning is 4, with peak values of Q'' occurring in the middle of each instar and with each successive peak higher than the previous one. The maximum values, occurring in the middle of each instar, are: 2.2 for the first, 3.6 for the second, 6.4 for the third, 10.6 for the fourth, and 14.1 for the fifth.

The values of the R.Q. during larval

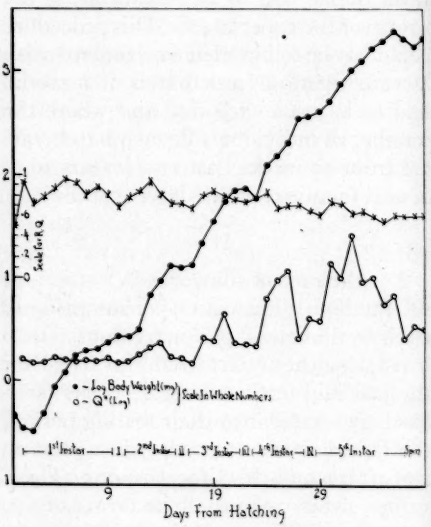

FIG. 2.—The weight in logarithm milligrams per larva (●) log Q'' (cubic millimeters of O_2 consumed per 2/3 power body weight in milligrams per hour) (o), and R.Q. (×) of silkworm larva plotted against number of days from hatching. Number and duration of each molt are marked with horizontal bars and Roman letters.

life are also plotted in Figure 2, together with the growth data. It may be seen from that figure that there is a striking correspondence between the variation of the R.Q. with the occurrence of molting. In general, the minimum values for R.Q., about 0.7, are found at the time of molting, while the maximum values occur in the middle of instars associated with heavy feeding. The highest value for the first instar is 0.95; the lowest is 0.68, at the first molt. The maximum for the second instar is 0.94; the minimum, occurring at the second molt, is 0.72. The maxima for the third, fourth, and the fifth instars are, respectively, 0.83, 0.83, and 0.74, with minimum values of 0.73 and 0.6 at the third and fourth molts. The value of R.Q. remained at 0.6 during the 3 days of spinning.

After the completion of the cocoon, the weight of the larva fell to 930 mg., as compared to its weight on the last day of feeding, which was 2,418. Thereafter, the weight of the pupa decreased very slowly, to the neighborhood of 640 mg. at the time of the emergence of the moth.

The course of daily variation in the values of Q during pupation follows a U-shaped curve. The data for the Q values of a female pupa is given in Figure 3. The value of Q falls from 701 cu. mm. per pupa on the last day of spinning to a minimum of about 240 cu. mm. between the third and the twelfth days after the completion of the cocoon, after which the values gradually rise to 540 cu. mm. on the day before the moth emerges. The corresponding values of Q' are 0.4, 0.25, and 0.51 cu. mm. A slight rise in the value of Q may be observed at the interval between the sixth and the ninth days of pupation, but the rise is very insignificant. The values of Q', when plotted against the duration of pupation, show the same trend of U-shaped variation as for the Q values, but not as marked. In Figure 3, only the logarithm of body weight and of Q are given.

The R.Q. during pupation rises gradually from the low value of 0.59 at the end of spinning to 0.67 on the fifth day, and then sinks to 0.6 again on the twelfth day, after which there is a gradual rise to 0.75 on the eighth day. The R.Q. remains almost constant at this level until the time of the emerging of the moth.

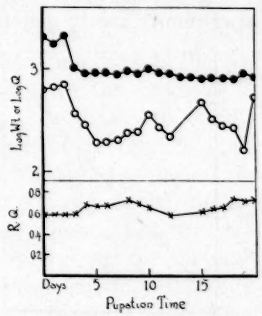

FIG. 3.—The weight in logarithm milligrams per pupa (●), logarithm of Q (cubic millimeters of O_2 consumed per individual per hour) (○), and R.Q. (×) plotted against pupation time in days, from first day of spinning to last day of pupation.

The weights of the adults of this race of silkworm are approximately 600 mg. for the female and 200 mg. for the male. There is no significant change in weight before and after fertilization; but, after the eggs are laid, the weight of the female is reduced to about 400 mg. Usually a batch of 400 eggs are laid totaling some 200 mg. After the eggs are laid, the adults gradually lose weight, and they die in 3–5 days. The values of Q' before fertilization are 1.36 cu. mm. per 24 hours for the male and 0.65 cu. mm. for the female, and those after fertilization are 1.1 cu. mm. for the male and 0.54 cu. mm. for the female. In the case of the female, the value of Q' after the laying of the eggs is 0.61 cu. mm. The higher values of Q' for the male adult are probably associated with its higher activity.

The values of R.Q. for both the male and the female are about 0.7.

IV

The literature pertaining to the respiratory activities of the silkworm up to 1931 has been reviewed by Needham (1931), who quotes the older work of Luciani and Piutti and Farkas on the production of CO_2 by the eggs of the silkworm during development. The results of our experiments are in general agreement with the course of CO_2 production obtained by these workers, with the minor difference that the curve for Q', instead of showing a continuous acceleration, becomes flatter on the last 2 days before hatching.

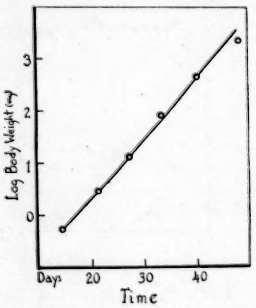

FIG. 4.—Logarithm of weight of larva on the first and last days of feeding and those at each molt plotted against time in days since hatching of silkworm larva.

The values of R.Q. for the developing eggs obtained by Luciani and Puitti are 0.97 at the beginning and rise past unity in the course of development to as high as 1.3. Our results are not in accord with these: the highest value of R.Q. in our case is 0.90, obtained on the second day of incubation. The R.Q. is about 0.75 between the third and the fifth days and 0.8 on the sixth day, with a minimum of 0.64 occurring on the eighth day. Based on the values of R.Q. which we obtained, it may be said that the silkworm probably consumes carbohydrate during the first 2 days of incubation, protein and fat during the remainder of its prelarval life, in the order named. The low value of 0.64 indicates the possible conversion of fat into carbohydrate on the eighth day of the developing eggs.

The series of S-shaped curves describing the growth in weight of the larvae could be described with some sort of equation as that proposed by Robertson for autocatalysis if so desired. But a simpler relation exists between body weight and days of development of the larvae, which may be seen from an inspection of Figure 2. If the logarithms of the weights at the first and last days of feeding and those at each molt are plotted against the number of days from hatching, a straight-line relation exists. Figure 4 gives a graphic presentation of this relation. This relation is similar to the rule proposed by Dyar, which states that the logarithm of some measurement of the larva at each molt bears a straight-line relation to the number of molts. This rule is the same as ours if the duration of each molt is of equal length, which is not the case in the silkworm.

From the course of the Q''/time curve for the larvae (Fig. 2) it may be said that in the earlier stages of development the body surface plays an important part in determining the intensity of respiration, so that the amount of O_2 consumed is proportional to body surface; and this, coupled with the comparatively light movement and feeding, renders the curve in the first 11 days practically a horizontal line, though there appears to be a slight rise in the curve on the fourth day of feeding, at the middle of the first instar. The rate is at its highest in the middle of any instar and at its minimum during molting. This difference is more marked the older the larvae, and is in good agreement with the increased activity and feeding during the instar, which

become progressively heavy with age, and with the cessation of feeding and activity during molting.

The values of R.Q. obtained during the course of larval development indicate that possibly fat is consumed during molting and that carbohydrate is consumed during the period of maximum feeding—at least in the first three instars. The possibility of protein being used during the larval period is, of course, not excluded. At the time of spinning, the R.Q. decreased to the minimum of 0.6, indicating the possible conversion of fat into carbohydrate and also probably into proteins.

An extensive study of the respiratory exchange in the silkworm has been made by Bialaszewiez (1937), which is available to us only in the abstracts. This worker reports a fall in the rate of O_2 consumption of 1.388 cc. per gram of body weight in the first molt to 0.626 cc. per gram of body weight during the fourth molt, and our Q' values show a similar trend of decline with age and are of approximately equal magnitude. The R.Q. which Bialaszewiez obtained varied from 0.5 to 0.99 during the period of development, falling to a minimum of 0.6 during pupation, with which our results are in general agreement.

Much interest is attached to the metabolism during metamorphosis, especially the chemical events taking place during pupation; and the literature on this subject is summarized by Needham (1931). The only data which are given are those obtained by Bataillon and by Luciani and Lomonaco some fifty years ago, on the production of CO_2 by silkworm pupae. The more recent work is that of Bialaszewiez (1937). The U-shaped Q/time curve which we obtained is in general agreement with those obtained by the Belgian and the Italian workers.

SUMMARY

Observations are made simultaneously on the growth and respiration of the silkworm *Bombyx mori* during its entire life-cycle. The weight of the eggs, after being taken out of cold storage, decreases steadily from 0.49 mg. per egg on the first day to 0.46 mg. on the tenth, the day before hatching. The weight of the larva increases from 0.35 mg. on the first day of feeding to 2,418 mg. on the last day of feeding in a series of five S-shaped curves associated with the five instars. The weight of the larva at the end of spinning is reduced to about 930 mg. The weight of the pupa is about 900 mg. on the fifth day of pupation and declines to about 850 mg. at the end of pupation. The approximate weights of the adult moths are 200 mg. for the male and 600 mg. for the female, with no significant change before and after fertilization. The weight of the female after laying a batch of about 400 eggs, totaling some 200 mg., is reduced to 400 mg.

The rate of O_2 consumption expressed in cubic millimeters per milligram of fresh weight per hour (Q') for the eggs increases in an accelerating manner from 0.21 on the first day of incubation to 0.72 on the day before hatching. The values for the R.Q. obtained during this period indicate that the eggs use carbohydrate at the beginning of their development, then protein and fat, with possible conversion of fat into carbohydrate at a certain period of development. The rate of O_2 consumption, when expressed in terms of body surface (Q''), shows a certain degree of regularity which suggests a "basal" rate of 1.75 cu. mm. in the first instar and 1.67 cu. mm. for the first molt, 2.17 cu. mm. for the second molt, 3.5 cu. mm. for the third molt, 4 cu. mm. for the fourth molt and the first day of spinning. These "basal" rates are raised in the

midst of each instar, owing to feeding and activity; and the peak values for the successive instars are: 2.2, 3.6, 6.4, 10.6, and 14.1 cu. mm. The values of R.Q. obtained during the period of larval life indicate that fat is consumed at each molt, while carbohydrate is consumed at the time of maximum feeding. The low value of 0.6 for the R.Q. during spinning indicates conversion of fat into carbohydrate and possibly also into proteins.

A characteristic U-shaped curve is obtained for the rate of respiration during the period of pupation, with the minimum occurring between the third and the twelfth days. The values for the R.Q. during this period varied from 0.6 to 0.75.

A straight-line relation is obtained when the logarithms of the weights on the first and last days of feeding and those at each molt are plotted against time in days following hatching.

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PHYSIOLOGY OF THE SILKWORM

II. MECHANISM OF SILK FORMATION AS REVEALED BY X-RAY ANALYSES OF THE CONTENTS OF THE SILK GLAND IN BOMBYX MORI

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I

THE silk fiber as secreted by the domestic silkworm, *Bombyx mori*, has a definite chemical composition and physical structure. Chemically, silk is composed of 70–75 per cent fibroin and 20–25 per cent sericin, both of which are proteins. The former, which makes up the bulk of the fiber, is insoluble, while the latter is soluble in hot or slightly alkaline water. X-ray analyses of many varieties of silk fibers made in the last decade or so reveal a definite crystalline arrangement of fibroin, which is essentially the same for all the varieties of silk tested—even for that of the spider (Astbury, 1933; Herzog and Jancke, 1927). While we are comparatively well informed about the chemical and physical nature of the silk fiber after it is secreted from the silkworm, very little is known regarding the state of fibroin inside of the silk-secreting glands; and the mechanism involved in the transformation of the gelatinous substance into the orderly arranged crystalline fiber is still a matter of conjecture.

In the mature silkworm immediately before spinning, the most conspicuous organ in the body is the pair of silk-secreting glands. The translucent gland may be divided into three parts, in correspondence with its external appearance. The posterior section, which is by far the

longest, is slender and cylindrical and is commonly believed to be responsible for the secretion of silk. The middle section, which is about one-fourth the length of the secreting portion, is very much thickened and is commonly associated with storage. This middle portion tapers into a short and narrow duct, which opens to the outside through the oral cavity. During the process of spinning, the silkworm attaches the end of the silk, secreted from the duct, to some object and begins a series of figure-eight movements, drawing the gelatinous contents from the broadened middle portion through the duct. The thin thread, when near the end of the duct, passes through a muscular press which squeezes together the two strains (brins) from the pair of glands into a single fiber. Thus, in spinning, the silk fiber is subjected to a tension along its long axis and a compression normal to this force.

When seen under the microscope, the contents of the second and third parts of the gland are gelatinous with no definite shape. In the duct the contents, probably because of the shape of the former, assume a threadlike form which is smooth and straight when moist but which may assume the shape of spiral when dry. When the gland is severed from the body of the silkworm, silklike threads may be spun artificially out of the open end of the duct, as well as from the middle portion, but not from the third long and slender part. When moistened with dilute acetic acid, the whole gland, and particularly the middle portion, may be drawn out into a single fiber of about a meter in length and 2 mm. in diameter. When this cylindrical thread is stroked or rubbed along its length while still moist, a flattened ribbon 1–2 mm. in width results. The gland may be pressed, while in a moist state, into a flat band. When left to dry, the gland loses water and turns into a horny brown structure preserving the original form.

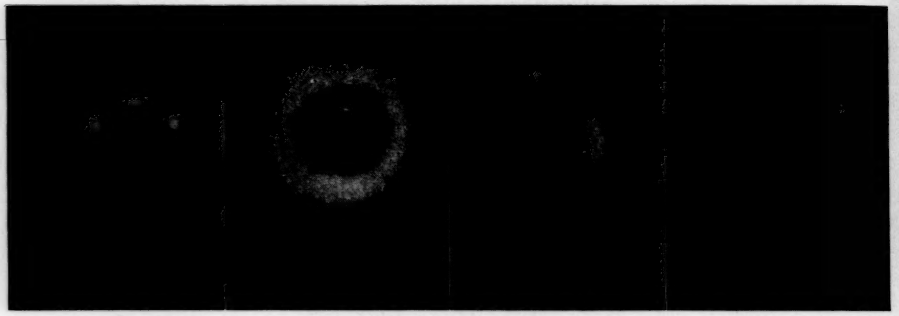
This paper presents a series of X-ray diffraction pictures of the contents of the silk-secreting glands treated according to the procedures described above, in an attempt to obtain some insight into the physical state of fibroin in the gland and into the mechanism involved in the transformation of the amorphous glandular contents into the orderly crystalline arrangement in the silk fiber. X-ray diffraction pictures of dried and *in vivo* silk glands were given in a brief note by Brill (1930) over a decade ago; but a detailed study of the problem, as proposed in this account, appears to be lacking in the literature.

II

The silk-secreting glands of mature silkworms, at the time of spinning, were dissected out of the body. They were used either dry or in the moist condition; if the latter, they were kept moist during the course of irradiation by the frequent addition of distilled water on a cotton wad in contact with the gland. The three portions of the gland were exposed separately. For the broad middle portion the contents may be easily separated from the gland when dry, and it was so used in obtaining the diffraction pattern for the dried materials of this section. For the wet glands and for the other two sections of the gland no attempt was made to separate the contents from the gland. Diffraction patterns were also obtained for threads artificially spun out of the duct and out of the middle portion of the severed gland, for the flattened glands, and for the glands drawn out into a cylindrical thread or into a flattened ribbon. In the case of the flattened gland not subjected to drawing, the incident radiation is normal to the flat surface, while in the drawn ribbon the incident radiation is on

the thin edge, parallel to the flat surface and normal to the long axis.

The fibers or glands were arranged parallel to one another on a suitable support, packed to a thickness of about $\frac{1}{2}$–1 cm. They were placed 3.5 cm. from the film and were irradiated with molybdenum radiation from a standard X-ray apparatus, and Laue diffraction patterns were taken with the customary method. An exposure time of from 8 to 10 hours was used, depending on the thickness of the materials.



a *b* *c* *d*

FIG. 1.—X-ray diffraction patterns for the contents of the silk-secreting glands of *Bombyx mori* and for silk fibers. *a*, Pattern for natural silk; *b*, pattern for wet gland (and for water); *c*, pattern for dried gland, middle portion, glandular contents only; *d*, pattern for cylindrical thread drawn from gland.

III

The usual diffraction pattern for silk fiber (Astbury, 1933; Kratzky and Kuriyama, 1931) was obtained with natural silk (about 20 μ in diameter), as well as with silk ribbons obtained by drawing and flattening the middle portions of the glands. The same pattern, though less defined, is obtained for the threads (7 μ in diameter) artificially spun out of the severed duct. The pattern for these are shown in Figure 1, *a*, which is that obtained with natural silk.

When moist, all three portions of the glands show the same pattern (Fig. 1, *b*), that of a rather well-defined ring, which is also given by a piece of agar (2 per cent) suspended in water. This indicates that for the wet gland the contents in all three portions are in aqueous colloidal solution, so that only the pattern for water is obtained.

For the three portions of the dried glands and for the thread artificially spun from the broad middle portion of the severed gland (140 μ in diameter) the diffraction patterns are the same and are in the form of a single ring (Fig. 1, *c*). But this ring is smaller than that for water shown in Figure 1, *b;* and its diameter is the same as the distance between the two inner equatorial spots for the silk-fiber pattern (Fig. 1, *a*). This indicates that, when dried, the contents of the three portions of the silk gland are the same in chemical composition and are the same as that for silk fibroin, except that in the former the molecules or molecular aggregates are in less defined arrangement, as against the high degree of crystalline arrangement of the molecules and molecular aggregates in the silk fiber. The same pattern is obtained with the flattened gland by pressing it along the entire length but without subjecting it to tension.

That the ring pattern is identified with

the glandular contents, and not with the gland itself, may be shown by the fact that the pattern as shown in Figure 1, *c*, is obtained for the dried contents of the middle section alone, without the glandular wall. The reason that a difference exists between the diffraction pattern for the threads artificially spun out of the duct and those spun out of the middle portion of the gland may be explained by the observation that, in spinning the thread out of the narrow orifice of the duct, more tension is needed than for pulling the thread out of the middle portion. Thus, in the former the thread, as it is being pulled out of the duct, is subjected to tension, and perhaps also to pressure on the side due to contact with the walls of the narrow duct, a condition very close to the process of natural spinning. In pulling the thread out of the middle portion, the force used may not be sufficient to effect an orderly arrangement of the fibroin molecules, whereas the tension used in pulling the thread out of the narrow duct is sufficient to effect such an orderly arrangement, so that the pattern for the latter resembles that of the silk, although not so well defined.

When the entire middle portion of the gland is drawn into a cylindrical thread without applying pressure on the side, a diffraction pattern intermediate between that for the silk and that for the dried glands results (Fig. 1, *d*), in which the small ring for the dried gland remains but is accentuated by two spots corresponding to the two inner equatorial spots for the pattern of the silk fiber. This indicates that the cylindrical thread has a crystalline structure approaching that of the silk fiber.

IV

The fact that the three portions of the silk-secreting gland of the silkworm give the same diffraction pattern, whether wet or dry, and the fact that the pattern for the dried gland bears a resemblance to that for silk fiber indicate that the chemical nature of the contents in the three portions of the glands are not only the same among themselves (cf. Brill, 1930; Cheng and Tang, 1943) but are the same as that for the silk fiber. The main difference between the contents in the silk-secreting gland and the fibroin of the silk fiber is in the degree of coagulation or consistency of the material and in the orderliness of the arrangement of the molecules. For this reason we may speak of the contents of the silk gland as "fibroinogen," which is similar to fibroin in chemical composition, differing from it only in consistency and in the orderliness with which the molecules are arranged. The "fibroinogen" may be considered to be in aqueous colloidal solution, much as agar is suspended in water. When this gelatinous mass of "fibroinogen" is subjected to tension and pressure in such a way as to effect an orderly orientation of the molecules, and when this orderliness is preserved by coagulation of the substance, crystalline fibroin of the silk fiber is the result.

The mechanism of silk formation in the silkworm, as revealed by the diffraction patterns presented in this account, may be pictured in the following manner. The silk gland may be compared to a large ovoid reservoir, connected to a long stream supplying the reservoir with logs floating in and on the surface of water. The reservoir has a long and narrow exit in the form of a canal, with the locks at its further end, preceded immediately by a strip of narrow constriction the width of which is much smaller than the lengths of the logs but larger than the diameters of their cross-sections. As the stream flows past this bottleneck, the logs are lined up with their long axes in the direction of the stream and, because of the

constriction, are packed in a rectangular block of many layers thick. The tension is supplied by the pull of gravity on the water and the logs, and the pressure for the packing of the logs is supplied by the narrow constriction. We may further imagine that there exists a refrigerating system immediately outside of the locks which freezes the stream and the logs contained in it into a gigantic thread and that the latter is drawn away as such by a system of belt conveyors.

If an X-ray picture were taken of the water-filled reservoir, we would find that, owing to the random arrangement of the logs in it and because of the enormous amount of water compared to the number of logs present, the diffraction pattern would be predominantly that for water. If the water were evaporated off, leaving the logs piled up in the reservoir in a random manner, with perhaps occasional groups of logs in some orderly arrangement, the diffraction pattern would be that of a ring, characteristic of the powder or of noncrystalline solids. These same pictures would be obtained with the source or with the canal, as long as the logs are not arranged in any definite pattern before they reach the narrow constriction and the locks. But if an X-ray picture were taken of the stream outside the locks, with the orderly arranged logs frozen therein, the pattern would be that of spots obtained with silk fibers.

The above picture of the mechanism of silk formation in the silk-secreting glands of *Bombyx mori*, clear though it is, is still incomplete. The mode of entrance of the protein nitrogen into the glands from the body fluid and the mechanism of such a rapid process of coagulation as seen in the formation of silk still remain to be elucidated by the labors of the physiologist and the colloid chemist.

SUMMARY

Roentgen-ray diffraction patterns obtained on wet and dried silk-secreting glands of *Bombyx mori* show that the chemical nature of the contents are essentially the same for all the three parts of the gland, including the duct, and that in the moist condition the contents are in aqueous colloidal suspension. The contents in the gland differ from the silk fiber only in being uncoagulated and in having the molecules or molecular aggregates in random arrangement, as against the orderly arrangement in the silk fiber. In the former the randomness of arrangement gives only a water pattern for the wet gland; and for the dried glands, in which the molecules possess a certain degree of orderliness, the diffraction pattern is that of a ring the diameter of which is the same as the two inner equatorial spots in the spot pattern for the silk fibers. The transformation of the amorphous gelatinous glandular contents into the orderly crystalline arrangement of the molecules in the silk fiber is accomplished simply by applying tension along the long axis of the fiber and by applying pressure on the side in a direction normal to the tension.

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AGGRESSIVE BEHAVIOR AMONG VERTEBRATE ANIMALS[1]

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INDIVIDUAL aggressiveness, as shown by threatening or fighting, plays a central role in vertebrate societies and populations. It also occurs in a number of insects, but the matter has not been generally investigated in other groups of animals. It is possible that aggressiveness in a more subtle form may be expressed simply by independence of action, and its opposite, submissive behavior, merely by avoidance of another animal. Any general study of the matter in vertebrates must at present be largely limited to the more obvious expressions of aggressiveness. Social control by means of aggressive behavior is to be distinguished from social dominance, which is a more general term and refers to the determination of behavior of given individuals by other individuals, whether by aggressive behavior or by other means.

The general purpose of this article is to attempt to place aggressive behavior in its proper perspective as an aspect of the biology of vertebrate animals and so to gain some idea of the generalizations possible and of the current problems concerning this trait. This purpose involves a survey of the role of aggressive behavior in the ecological pattern of living systems, of the associated psychological, physiological, and genetic mechanisms, and of the evolutionary changes in aggressive behavior patterns. It must be recognized at the outset that, as a result of the undeveloped nature of this field of study, any suggestions which are made are often to be regarded as a framework for continued research rather than as well established rules.

Living systems are organized into patterns in which integrated systems at one level of organization may themselves be units of a more inclusive grouping, as is illustrated by the following series: individual, social group, population, and animal community. The first problem is to clarify the role of aggressive behavior at each of these different levels of organization.

ROLE OF AGGRESSIVE BEHAVIOR

I. WELFARE, SURVIVAL, AND REPRODUCTION OF INDIVIDUALS

Individual aggression in vertebrates is frequently expressed in two special forms, which are not necessarily mutually exclusive and which include (*a*) defense of a given area (territory) and (*b*) hierarchies of precedence within social groups. These hierarchies consist of the disposition of two or more animals, or

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animal groups, in ranks or orders, each subordinate to the one above it with respect to the aggressive-submissive dominance relations. Examples of the two different kinds of behavior are exhibited within each of the classes of vertebrates, with the possible exception of the Amphibia.

Good reviews of territorial relations have recently appeared for fish (Noble, 1938) and for birds (Nice, 1941). The present survey places more stress on social hierarchies under more or less natural conditions, strongly supplemented by observations on captive or domestic animals. This procedure may help to close the gap between field and laboratory studies of social organization of vertebrate animals by demonstrating that many similarities, as well as differences, exist in the way that animals behave in the field and in the laboratory. Social hierarchies have been described for most domestic animals and have often been observed among those in cages or in pens and among fish in aquaria. Most of the field studies have dealt with birds and mammals.

Aggressiveness may lead to the establishment of high social rank within a group; and high rank frequently gives precedence to food, to mates, and at times even to territory. However, in the last case the reverse is often true; and possession of a territory usually means social domination of that territory, so far as the given species is concerned, and tends to prevent formation of a rigid social hierarchy.

SOCIAL HIERARCHIES AND THE INDIVIDUAL

Social rank is often, perhaps generally, decided by fighting, bluffing, or passive submission at the initial encounter between any given pair of individuals or by an early series of such encounters. This holds almost diagrammatically with adults of the common domestic fowl (Schjelderup-Ebbe, 1922, 1935; Collias, 1943 and citations); it has also been observed in captivity for diamond doves,[2] for mice (Uhrich, 1938; Ginsburg and Allee, 1942), for macaques (Maslow, 1940), for chimpanzees (Crawford, 1942), for the American chameleon (Evans, 1936*a*), and for the fish *Platypoecilus* (Braddock, 1942). It has been noted in the field for the birds called "blue tits" (Colquhoun, 1942); during field studies on various infrahuman primates Carpenter (1942*c*) observed that fighting or the threat of fighting was important in helping to establish dominance status.

In general, when a number of strange chickens or fish (Braddock, 1942) are grouped in the laboratory, a period of active fighting may precede the later period of greater social stability; this has been observed under natural or field conditions for valley quail (Emlen, 1939; Howard and Emlen, 1942). Among valley quail partially established members of a covey dominate aliens of subsequent introduction (Howard and Emlen, 1942). Strangers among the vertebrates appear almost invariably to be attacked when they try to enter small groups organized on a hierarchical basis (Lorenz, 1931; Odum, 1941; Carpenter, 1942*b*; Alverdes, 1935). If they are permitted to enter, they tend to be relegated to the bottom of the social order, and they may gradually fight their way up—for example, as in winter flocks of chickadees (Odum, 1941).

Once social rank is established, it is maintained by the habit of subordination of those in lower positions, reinforced by threats or punishment dealt

[2] Results of experiments that are unsupported by citations and based on my own observations, hitherto unpublished.

out by those of higher rank. The exact method of coercion varies with the special weapons of the species. "Tension" often appears to be greatest between closely ranked individuals and may be shown by mutual avoidance or tendencies toward revolt, as has been noted in chickens (Schjelderup-Ebbe, 1935), or by the increased frequency of blows dealt to immediate subordinates, as has been observed in fish (Noble, 1939), jackdaws (Lorenz, 1931), and chickens.[2]

Revolts and reversals in the social scale are not very common in stable groups and usually require active battle. Shoemaker (1939*b*) noted that canaries of low rank, when injected with testosterone propionate, were subjected to increased pecking by the given despot shortly before reversal of their relative ranks took place. Under similar conditions, low-ranking hens revolt and reverse position most often with reference to the individual immediately above the rebel in the general social scale (Allee, Collias, and Lutherman, 1939).

There are a number of ways in which an animal of inferior caliber but especially favored by circumstances may gain more or less temporary ascendancy over another superior to it in most respects. These have been described for chickens by Schjelderup-Ebbe (1935). Our observations agree with those of Murchison (1936) and of Sanctuary (1932) that complex, triangular hierarchies, such as are common in all but very small flocks of chickens, as a rule tend to simplify and straighten out with time, presumably because each individual gravitates toward its appropriate place in the scale of relative aggressiveness. This important phenomenon deserves additional study.

In laboratory studies of primates, precedence to food is commonly used as an indicator of social dominance; and such precedence, according to social ranking based on aggressiveness, has been noted for certain other mammals (Winslow, 1938; James, 1939), for fish (Noble, 1939), for turtles (Evans, 1940), and for many birds. Thus the struggle for food among nestlings of the black-crowned night heron leads to a hierarchy of dominance based on aggressive behavior (Noble, Wurm, and Schmidt, 1938). Under somewhat more natural, free-ranging conditions, precedence to food according to social level has been observed in winter flocks of chickadees (Odum, 1941), blue tits (Colquhoun, 1942), and other birds (Nice, 1929) and in various primates (Carpenter, 1942*c*).

The degree of competitive action may be greatly increased by hunger—for example, in laboratory groups of monkeys (Maslow, 1936*a*), chimpanzees (Nowlis, 1941), rats (Bruce, 1941), and chickens. The frequency of pecking of subordinates can readily be increased several fold in flocks of hens by placing the birds on short rations.[2] In the field, muskrats may be crowded by drought into small waterholes without severe friction; but, if there is also a food shortage, as is often the case, aggressive interaction may be severe and often lethal (Errington, 1939*a*).

Adverse previous experience may be an important factor in some cases. Chickens that have been strongly persecuted learn not to come to the food hopper until the dominant birds have finished eating. Starving birds frequently feed despite blows from their despots. Among chimpanzees extreme food deprivation by itself may not be sufficient cause for a subordinate to respond positively in food competition with a dominant animal unless there is high expectancy of success (Nowlis, 1941). Apparently, the balance between fear of despots and degree of hunger is an

important element in food competition, at least as seen in the laboratory.

Satisfactory studies on the possible survival value of high rank in relation to food shortage in nature do not seem to have been made. Winter starvation is an important decimating factor in populations of northern bobwhite quail, and it is also known that well-fed birds withstand adverse weather conditions much better than do poorly nourished individuals (Errington, 1939*b*). Recent evidence gathered in this laboratory suggests that in flocks of hens on short rations birds of high rank usually get more to eat and maintain weight better than do birds of low rank. Whether this is true or not among quail and other birds in nature is a problem for investigation.

Individual survival value would favor the leaving of more descendants by such individuals, and the same end may be more directly attained by increased success in mating. The dominant male in caged groups of the lizard, *Anolis carolinensis* generally mates most frequently (Noble and Greenberg, 1941*a*). Laboratory studies on domestic cocks in relation to their place in the social hierarchy (Guhl, 1941) have shown a decidedly greater frequency of mating by males high in the social hierarchy. This has been strikingly noted in field studies of sage grouse (J. W. Scott, 1941, 1942) and more precisely in rhesus monkeys (Carpenter, 1942*b*). The males of many polygynous ungulates will herd together as many females as they can defend from other males (Alverdes, 1935; Darling, 1937). In the late winter flocks of the monogamous Gambel's quail a female will often pair off with the winner of a fight, even after pair formation with the loser had apparently recently taken place (Gorsuch, 1934).[3] The female of the salmon, which is the sex that builds the nest, may be attended by a succession of males as the larger, cruising males drive off smaller rivals and usurp their position (Noble, 1938).

Females may compete among themselves for mates, as in the case of the rhesus monkey (Carpenter, 1942*a*). Females of the monogamous gibbon probably drive maturing daughters out of the family group, as the males do their sons (Carpenter, 1940). Defense of the male mate against other females is common among birds, as in the willow wren and snow bunting (Tinbergen, 1936); and mild aggressive competition between females for the attentions of a male has been observed for the sage grouse, which is characterized by promiscuous polygyny (J. W. Scott, 1942). In the European three-spined stickleback the most sexually advanced female dominates and drives other females from the immediate vicinity of the nest in which she intends to lay (Noble, 1938). Unmated jewel fish in breeding condition confine their attacks to members of the same sex; but, after pairs are formed and the members of a pair have learned to know each other as individuals, they drive off other jewel fish from their territory, regardless of sex (Noble and Curtis, 1939). Such mutual jealousy in the early stages of pairing probably helps to facilitate monogamy.

With many vertebrates it is known that fighting between males greatly increases in frequency and intensity in the presence of females. Food or territory as complicating factors can be clearly ruled out in some cases. Food may be largely ignored during the breeding season by male fur seals (Alverdes, 1935) and red deer stags (Darling, 1937), especially during the period of intense competition for females. Many monogamous male

[3] "In a mating of long duration however, this may not hold, and both hen and cock frequently unite to drive away any intruder on their domestic tranquility" (Gorsuch, 1934).

birds are known to become much more aggressive toward other males after pair formation is definitely effected; and some birds, like the willet, may pair, and the male will then defend the female before establishing a territory (Lack, 1939*a*). The Sierra Nevada rosy finch is said to have no fixed territory, and defense reactions are displayed by a paired male only when another male approaches his mate (Twining, 1938). Fighting between males in the presence of females is not inevitable, since, among rhesus monkeys, a subordinate male may consort first with a female if there is a plentiful supply of females, but, if there is only a single female available, she is always possessed first by the dominant male of the group (Carpenter, 1942*b*). The same author (1934) found no fighting over females in groups of howler monkeys.

Adverse previous experience with sex rivals may be important. Subordinate cocks of the domestic fowl, after continued persecution and suppression by the dominant cock of a flock, will tread much less frequently, even when tested in the absence of the dominant cock, or with different hens, resulting in what Guhl (1941) has called "psychological castration." According to A. A. Allen (1934), ruffed grouse which have been strongly subjugated (under laboratory confinement) may die shortly thereafter, apparently from some obscure mental shock rather than from wounds or food deprivation; the dominant grouse survive.

TERRITORY AND THE INDIVIDUAL

Details of the operation of territorial mechanisms have been most thoroughly worked out for birds. A high place in the social order may at times give precedence to the occupation of open territories, but eviction of a bird from its territory by another member of its species does not seem to be very common in nature. In winter flocks of chickadees Odum (1941) found that the three top-ranking males were the ones that remained on or near the winter feeding grounds to breed in the following spring. It is possible that here, as in blue tits, these birds were dominant in the winter flock because they had held near-by territories in the preceding spring rather than because of innate aggressiveness. There is always at hand a reservoir of young birds; these birds, usually low in the social order, are available to supply replacements for vacated and suitable territories within the area covered by the flock. It remains to be determined whether such occupancy may take place according to social precedence in the pre-existing hierarchy of the winter flock.

In the case of migratory and many lek birds in which breeding or mating territories are set up anew each year, a complete and clear-cut social hierarchy may not be established before territorial claims are laid. In such cases possession of a territory often depends on priority in staking out the claim. However, early territorial boundaries are very labile and subject to reduction in size as later arrivals carve out places for themselves, which they must do by physical or psychological combat unless population density is low (Nice, 1937; Kendeigh, 1941). A high degree of aggressiveness is evidently of advantage in securing a foothold. During early spring, among prairie chickens there apparently is general fighting over the whole booming grounds as each cock establishes his place; but, once boundaries are set, each cock tends to remain in his own territory, where he is dominant (Hamerstrom, 1939). According to Chapman (1935), a socially subordinate male of Gould's manakin, a tropical lek bird, may not defend as

large a mating territory as a more dominant and more sexually active bird.

Territorial defense reactions tend to increase in frequency and intensity with crowding, as in the case of terns (Palmer, 1941) and house wrens (Kendeigh, 1941). As an opposite tendency, Kendeigh noted that the vigilance of territorial defense decreased as the birds learned each other's boundaries.

Possession of a territory gives precedence to food in that territory. This is important for birds which get their food within the territorial limits, especially for the nestlings (Nice, 1937). Compression of breeding territories in birds may be permitted to a considerable extent if the food supply is abundant, as in kestrels and white storks (Nice, 1941). Defense of territories is a phase of aggressive behavior which may lead indirectly to precedence in mating. In the song sparrow (Nice, 1937; 1941) the male arrives before the female in the spring, and the females come to those males which have established territories.

II. AGGRESSIVE BEHAVIOR IN RELATION TO STABILITY AND SUBDIVISION OF SOCIAL GROUPS

The term "social" has been loosely used and variously defined with reference to animals (Allee, 1938). Basically, the term signifies group co-operation and, in a broad sense, may refer to interpersonal co-operation at any level of organization. This section, for purposes of convenience, refers mainly to social groups the members of which live together and which in many cases move about as coherent units over a common area, as do flocks or herds, and whose integration appears to be primarily and essentially dependent on interindividual, rather than on habitat, stimuli. This latter attribute conforms to Wheeler's (1930) definition of animal societies. In many ways, perhaps, "society" would be the most satisfactory available term; however, it has been used with many different meanings, and, accordingly, the aggregations under consideration will somewhat arbitrarily be referred to merely as "social groups."

SPECIFIC TOLERANCES AND THE FORMATION OF AGGREGATIONS

Aggressive behavior can be regarded as asocial in so far as it acts to prevent, decrease, or disrupt the integration of vertebrate societies, and it can be regarded as social in so far as it furthers the integration and organization of such societies. Aggressive behavior often is at one and the same time an active force in the subdivision of societies and in the integration of the smaller units so formed. Social life becomes possible when social tolerance is greater than asocial tendencies within the group (Allee, 1931). Co-operation, as shown by the more widespread existence of social or subsocial aggregations of some sort, is more basic and widespread among vertebrate animals than is aggression. The individual aggressive tendencies which exist in a great many vertebrates and which might be strong enough to overbalance the generalized drive toward sociality are often counteracted by certain specific tolerances or attractions, with a resulting decrease in aggressive behavior. This, in turn, permits the formation of social systems of various sorts that may enter into competition with each other. These different social systems often represent different levels of social organization, which can be arranged in a rough order of increasing inclusiveness of the internal social relations.

At the individual level the existence of little or no tolerance results in solitary habits; for example, outside of the breed-

ing season shrews may kill other shrews encountered (Alverdes, 1935).

At the level of the social group, tolerance and attraction for the opposite sex leads to a mateship—for young to a family, for acquaintances (not necessarily of the same species) to acquaintanceship groups. Mutual tolerance in the face of a common enemy leads to the formation of a defense group such as is shown by a crowd of small birds mobbing a predator. These different types of relatively small and simple societies, while not necessarily falling into a progressively inclusive pattern with reference to one another, as arranged above, often do show increase in number of individuals and therefore in number of intragroup social relations. These various social units overlap; for example, the factor of acquaintanceship probably makes for increased tolerance in every case, but the acquaintanceship group, where each individual knows the others as individuals, is especially dependent on this factor. Tolerance for strangers, especially with increasing size of group or under suitable habitat conditions, makes possible formation of larger, often compound, societies, such as migratory flocks of birds, which may consist of acquaintanceship groups or family groups or both (Allee, 1931; Friedmann, 1935).

At the level of the species, tolerance for individuals or groups of the same species with increasing distance between them may result in organization of populations on a territorial basis. At the level of the animal community, tolerance for other species enables many individuals of diverse species to live together. Tolerance within each type of social unit may be greatly increased by decreasing the need for competition, i.e., under conditions of plentiful food supply, shelter, breeding sites, or mates. For example, male western fence lizards ordinarily hold separate territories; but, where food and shelter are abundant, several males may live in close association with one male dominant (Fitch, 1941). The controlling consideration is the balance between the degree of aggressive behavior of the members of a group and their mutual toleration, as shown objectively by their tendency to aggregate, whatever the mechanisms that are involved in either.

A CLASSIFICATION OF SOCIAL GROUPS AMONG AGGRESSIVE SPECIES OF VERTEBRATES

The following tentative classification of social groups according to the degree of integration and organization also affords a means of summarizing the more important literature which concerns social hierarchies of nondomestic vertebrate animals formed under free-ranging and natural or seminatural conditions.

A. Individual competition for food, mates, or territory dominates; group open, usually more temporary; fighting frequent.
   1. Toleration minimum; dispersed populations, and societies in the process of formation or disintegration. Nice (1941) has classified territories among birds according to their size and the number of functions (mating, nesting, feeding) subserved; size of territory generally increases with number of its functions. Territorial rodents may have a considerable extent of more or less neutral area about their territories, wherein a definite chasing order is present, as in the case of the golden-mantled ground squirrel and of certain chipmunks (Gordon, 1940). Groups of more or less free-ranging American chameleons (Greenberg and Noble, 1942) and of western fence lizards (Fitch, 1941) may at times exhibit dominance hierarchies which seem to be based primarily on modified territorial relations. Among certain deer, antelope, gazelles, and buffaloes, the young males may unite to form bachelor packs in which there are no leaders and in which there is continual quarreling, especially during the mating season (Alverdes, 1935). Such disintegrating groups are

frequently found when males compete directly for mates as in late winter flocks of Gambel's quail (Gorsuch, 1934) and red-deer stag parties at the onset of the rutting season (Darling, 1937). In this category also belong the feeding assemblages where precedence is marked, especially in heterospecific groups—for example, different species of birds at a winter feeding station (Nice, 1929; Colquhoun, 1942).

2. Toleration greater and group consequently more evident and coherent. An incomplete social hierarchy may be formed within the group; i.e., dominance relations may not be settled between all individuals. Mating assemblages of sage grouse (J. W. Scott, 1941, 1942) and many feeding assemblages, where food is plentiful and individual competition is relatively low, are appropriate examples. Female *Anolis carolinensis* (confined under rather free-ranging conditions) may fight among themselves in a male's territory, and the resultant order may be a straight-line hierarchy (Greenberg and Noble, 1942).

B. Social group dominates and moves as a more or less coherent unit over a common area; individual composition of group more consistent, and dominance relations between individuals generally stabilized in a social hierarchy.

1. Social hierarchy evident within group.

a) Social order less stable; group temporary and semiclosed. Examples are winter flocks of chickadees (Odum, 1941, 1942) and blue tits (Colquhoun, 1942). Coveys of valley quail (Emlen and Lorenz, 1942) may fight as a group at times, and they represent a transitional type to the next category.

b) Social order more stable; group more permanent and more nearly closed and may act as a unit to drive invaders off of a common territory; some division of labor in the form of leaders or sentinels. Hordes of rhesus monkeys where the dominance of the group seemingly depends on the dominance of the supreme despot (Carpenter, 1942*a*, *b*, *c*). Family groups of gibbons where the dominance of the group depends to a large extent on size and aggressiveness of the group and proximity to the territorial center of the group (Carpenter, 1940). Family groups of full-grown blue geese where the defended area or sphere of influence moves with the group (Jenkins, 1944; Hale, 1941, unpublished manuscript).

2. Exercise of aggressive relations within the group largely suspended; group closed, permanent, highly social, with division of labor, and frequently acting as a unit to drive intruders off a group territory.

a) Exercise of aggressive dominance relations generally pronounced only between closely ranked individuals. This is a transitional type and is found among the colony-nesting jackdaws (Lorenz, 1931, 1934, 1935).

b) Exercise of aggressive dominance relations within group not very evident, or suspended. Howler-monkey clans where the males may share the same female peacefully (Carpenter, 1934), and possibly societies of the cuckoo-like anis in which several birds may lay and incubate in the same nest (Davis, 1942). The family in blue geese (Jenkins, 1944) until the young begin to mature. Permanent sex pairs, such as those of blue geese, which involve both physiological and morphological division of labor, with the preceding, represent the better-integrated types of social groupings among subhuman vertebrates.

The degree of aggressiveness and the strength of the territorial instincts determine to a large extent the nature of the dominance relations seen among many caged animals. Laboratory mice (Uhrich, 1938) and captive lions (Cooper, 1942), both of which are very aggressive toward other members of their species, show a monarchistic type of social order in which the despot tends to inhibit aggressive relations between his subordinates. This is the case in caged American chameleons (Evans, 1936*a*), which are strongly territorial in nature. In typical territorial passerines, such as white-throated sparrows (Wessel and Leigh, 1941), white-crowned sparrows, and

towhees (Tomkins, 1933), in fair-sized cages, dominance relations between subordinates are permitted more freely and a peck-right organization exists. In other words, in flocks organized by peck-right, subordinate birds do not, as a rule, peck birds above them in the peck-order. In birds which normally hold small territories even when in fairly small cages, such as pigeons (Masure and Allee, 1934; Diebschlag, 1941), ring doves (Bennett, 1939), parrakeets (Allee, 1938), and canaries (Shoemaker, 1939*a*)—all birds which flock closely—more or less asymmetric peck-exchange is the rule (Allee, 1938), and this has been called "peck-dominance." But, as Allee (1942) has recently pointed out, when territorial relations are involved it is difficult to ascertain the most aggressive individuals, since relatively unaggressive birds tend to remain within their own territory, where they win the majority of their encounters. By crowding canaries into still smaller cages, peck-dominance may be changed into peck-right (Shoemaker, 1939*a*); or the same thing can be done in ring doves by increasing their aggressiveness through androgen injections (Bennett, 1940).

Reasons other than those associated with well-established territory may be given for a peck-exchange type of relationship: a continuous series of fights which may eventually be fatal, as in *Betta* males (Noble, 1938, 1939); sham battles, especially seen in young animals, possibly territory of brief duration (Tomkins, 1933); co-operative attacks giving temporary dominance over a despot (Hale, 1941, unpublished manuscript); tolerance by the despot; and reverse pecks, as sometimes seen in the domestic fowl,[2] many of which are perhaps to be regarded as mistakes of the subordinate. It remains to be seen how frequent and important such variations might be under natural conditions.

Aggressive dominance relationships may be suspended by some animals when in very small cages. Among captive lions it appears that serious fighting will not take place in close quarters. But, if two strangers are housed together, they will begin to fight as soon as they get into an outside inclosure (Cooper, 1942).

ASOCIAL ASPECTS OF AGGRESSIVE BEHAVIOR

Any changes in aggressiveness of individuals influence the degree of social integration. Both absolute and relative levels of aggressiveness within a group are important. Among chickens, flocks composed only of cocks have a less stable order than that which characterizes flocks of the less aggressive hens (Masure and Allee, 1934). Markedly increasing the aggressiveness of low-ranking hens by injecting them with testosterone propionate caused them to rise in the social order of hens (Allee, Collias, and Lutherman, 1939). When the ovaries were removed from 6 birds selected from various social levels in a flock of 12 pullets, all of the operates fell below the intact birds, but they retained the same social rankings relative to each other.[2]

Both psychological conditioning and physical maturation influence the amount of intragroup aggression and are important factors in the establishment of a peck-order among chickens. In a flock of hens an initial period of fighting and social instability is followed by the establishment of a more rigid social order and, finally, in the absence of special disturbing factors, by an amelioration of dominance relations and increased tolerance of subordinates. However, baby chicks do not fight and have no dominance hierarchies based on aggressiveness.

Physiological changes induced by the environment may increase intragroup aggression and, correspondingly, decrease social integration. Winter flocks of birds may break up on a warm day into sex pairs, or males may occupy territories; with a succeeding cold spell the flock may reform, the individual territories be released, and the sex pairs be disunited (Nice, 1937). At the same time the progressive recrudescence of the gonads steadily forces a trend toward disruption of the winter flock, toward individual territoriality, and toward sex-pair formation. Hunger, as has been pointed out, is a potent factor helping to determine the degree of intragroup aggression. It cannot be too strongly emphasized that a dynamic picture should be maintained with respect to the degree of integration of any given group. It might have been possible to remove the qualifying terms in the foregoing classification if the phenomena under consideration were more rigid and less subject to variation with the environmental situation.

Numbers present exert a general influence on the stability of a social group. With the addition of each new individual the number of specific intragroup paired relationships increases disproportionately, as noted by Carpenter (1940) in this connection, by use of the formula $N(N-1)/2$. For example, the number of such relationships rises rapidly from 10 in a group of 5 animals to 45 in a group of 10 animals. In large acquaintanceship groups there is probably more fighting, as in chickadees (Hamerstrom, 1942); triangular dominance relationships are much more common; and it takes much longer for the social hierarchy to become stabilized. Our observations agree with those of Schjelderup-Ebbe (1935) that straight-line dominance is rare in flocks of chickens with more than 10 birds. Murchison (1936), studying five groups of cockerels of 2–6 birds each, described a disproportionate relationship between the size of the group and the length of time it took for straight-line dominance to become established. By extrapolation to larger groups he predicted that in a group of 10 birds it would take about 15 months—a prediction not supported by observation in this laboratory even though the general principle is sound. With groups larger than about 20 the number of possible relations becomes so great that precise study of group organization becomes impractical. It would appear that with more highly organized groups the integration of a small stable group tends to break down with increasing size of the group, possibly because recognition of individuals becomes more difficult.

SOME SOCIAL ASPECTS OF AGGRESSIVE BEHAVIOR

Aggressive behavior may be regarded as social in some respects; for example, it may help set up social barriers which limit the size of small groups down to the point where effective group organization is possible. This is the point of view stressed in this paragraph; but it is also true that, in so far as it tends to prevent federation of such groups, aggression could be regarded as asocial. The density and mobility of the species population as a whole is often important in determining the extent to which social groups remain open. As a group becomes larger and more loosely integrated, it sooner or later passes the threshold for individual recognition; tolerance for strangers apparently then increases. At low densities in laboratory populations of mice Crew and Mirskaia (1931) and Retzlaff (1938) observed that the entrance of any newcomer was at once noted and that the subsequent fighting commonly continued until it had been killed; in higher densi-

ties the immigrant had a better chance of surviving. The newcomer loses himself in the larger group. In low-density populations of valley quail, trespassers from other coveys are recognized and excluded (Emlen, 1939; Howard and Emlen, 1942). Where the quail are abundant and covey contacts more frequent, social barriers are less rigid.

The arrangement of social groups according to the degree of integration shows that, as egocentric intragroup aggression declines, co-operation in intergroup aggression increases and the amount of social service within groups increases. The gradual change from defense of individual pair territories to co-operative defense of communal territories—inversely related phenomena—is clearly seen in the various members of the Crotophaginae, a subfamily of cuckoos which includes the anis (Davis, 1942). Since group territories tend to be larger than individual territories, each individual within a society can range freely over a wider area. In so far as co-operative aggressiveness favors group life, it facilitates the various other benefits to be derived from this habit, such as increased safety from predators.

Social service within the group is itself frequently closely related to aggressive behavior. The despot in some species may be leader, as in kangaroos (Alverdes, 1935), or sentinel, as in familes of blue geese (Jenkins, 1944; Hale, 1941, unpublished). Jackdaws have a form of "police force" in which excessive despotism of any individual is blocked by co-operative attacks by the rest of the flock (Lorenz, 1931, 1935). Defense of the young by the parents is common from fish to man. Something akin to discipline of the young is seen in howler monkeys (Carpenter, 1934).

The "social service," so-called, may be rendered to a part of the group rather than to all the associated animals and may take the form of mutual aid in establishing social status. For example, in blue geese (Jenkins, 1944; Hale, 1941, unpublished) and monkeys (Maslow, 1936*a*) subordinates by a united attack may secure temporary dominance over a common despot. Among rhesus monkeys the male consort helps the oestrus female to rise in the hierarchy of females (Carpenter, 1942*a*), while in flocks of geese and jackdaws the female assumes the social rank of the male to which she becomes mated (Lorenz, 1935).

Certain aspects of territorial defense can be considered as different forms of social service; these are more or less specifically related, in various species, to copulation, nest-building, egg-laying, and successful incubation and rearing of young. Recent laboratory studies, although somewhat limited in this respect, indicate that domination of a territory may be essential to prevent interference with reproduction in territorial species—at least under the conditions of observation, for example, in jewel fish (Noble and Curtis, 1939), in canaries (Shoemaker, 1939*a*), and in robin redbreasts and chaffinches (Lack, 1940).

One form of social service of territory is that it helps prevent interference with normal functioning of a mated pair of individuals. Many male vertebrates attack or interfere with copulating males. If pigeons, which ordinarily hold small territories, are greatly crowded, the males continually interfere with each other's attempts at copulation, and the percentage of fertility is greatly reduced (Fulton, 1895, p. 437). Female pigeons may similarly attack a copulating female, pecking its head (Whitman, 1919); but such female intolerance among vertebrates seems, as a rule, to be less common or intense than in males.

Reiffer's hummingbird in Central

America may show nesting failures up to 50 per cent as a result of the stealing of nesting material from nests of other hummingbirds; this difficulty was apparently related to the lack of territorial defense reactions (cf. Davis, 1942).

In flocks of domestic hens which are not generally considered to be territorial birds, the low egg production of pullets at the bottom of the peck-order can be decidedly increased by removing them from the domination of their more aggressive flock-mates (Sanctuary, 1932). Individual territories would appear to help egg-laying, at least under certain conditions, in hens. Individual laying cages are often used in the egg-production industry.

Among fish, defense of the territory or nest may help prevent destruction of the eggs or young by other males or by fish of other species (Norman, 1931). In nature, terns, which are unable to maintain their small territories under very crowded conditions, desert their eggs and nests (Palmer, 1941). In monagamous birds where the males share the duties of incubation or care of the young, it may be of added advantage for the female to drive other females from the territory or neighborhood of her mate. The near presence of a strange, sexually active female may more or less inhibit broody behavior and crop growth in the male of an incubating pair of pigeons (Patel, 1936). Territorial defense by male birds may also be important in preventing the breakup of nesting by an intruding male (Nice, 1941).

The role of aggressive behavior in the integration of the sex pair deserves more detailed attention. Dominance relations between the sexes must often be established for harmony, but excessive aggressiveness toward the opposite sex is probably an obstacle to mating. Males generally dominate females, particularly during the breeding season; and female dominance over the male, while it may not be completely prohibitive, is said to hinder mating in caged monkeys (Maslow, 1936*b*) and in chickens (Schjelderup-Ebbe, 1935).

Courtship frequently serves to ameliorate the dominance relations and promote propinquity between the sexes. Many male birds, as well as some fish (Noble, 1939), practically cease to exercise aggressive dominance over the female during the breeding season. Male monkeys and apes grant the oestrus female greater feeding privileges (Carpenter, 1942*a*). The domestic cock calls hens to food, and more or less formalized courtship-feeding occurs in many birds.

Courtship behavior, which is usually presumed to be sexually stimulating, grades off indistinguishably and in a complex way into aggressive-submissive behavior. Adoption of a submissive display by the male night heron helps keep the female in his territory, so that pair formation may take place. The male then gains the dominance in subsequent mutual ceremonies. If a male night heron adopts a subordinate head position, he may be permitted to remain in another male's territory, and the two individuals may form a pair (Noble, Wurm, and Schmidt, 1938). According to Roberts (1940), the essential difference in the behavior of the sexes of the gentoo penguin, *Pygoscelis papua*, is that during the breeding season a male always tries to dominate weaker birds, while a female loses this dominating urge during the short period when fertilization must take place. Female terns inhibit attack from the male when pair formation takes place by adopting a submissive head posture, and the males inhibit male behavior in the females with an intimidation posture (Palmer, 1941). A rhesus monkey of either sex can often avoid

attack from another individual by presenting as for copulation (Maslow, 1936*b*; Carpenter, 1942*a*, *b*). This appears to be a sign of subordination, and in homosexual pairs of many vertebrates it is the dominant individual that generally mounts. Mounting by a subordinate monkey often stimulates the dominant to mount this subordinate, which then becomes more tractable (Maslow, 1936*b*). A number of female mammals when in oestrus exhibit mounting behavior; and oestrus-female mammals generally cease to fight, scratch, bite, or kick or persistently to avoid sexually driving males (Young, 1941).

AGGRESSIVE BEHAVIOR IN RELATION TO SUBDIVISION AND SPLITTING OF SOCIAL GROUPS

Aggressive behavior may play a role in the subdivision of large societies. The threshold for effective group organization varies with the capacity of the species, but most simple and relatively closed societies are small. Wing (1941), in an extensive numerical summary, has recently shown that winter flocks of birds in the majority of cases consist of two dozen birds or less. Probably even these, like larger groups, are often composed of subgroups. Fischel (1927) observed that a flock of 500 white leghorn hens broke up readily each day into open subgroups.

Favorable conditions of habitat permit crowding, while previous acquaintanceship leads to the consistent association of particular individuals to form a semiclosed group which may gradually merge into, and later split out as, a unit from the larger compound group; for example, large winter flocks of chickadees readily break up into subgroups with usually less than about 8 individuals (Wallace, 1941). Similar subdivision is seen in coveys of valley quail (Howard and Emlen, 1942), in coveys of northern bobwhite quail (Errington and Hamerstrom, 1936), and in herds of red deer which are composed of a varying number of family groups (Darling, 1937). Addiction to special places within the area ranged over by the entire group also favors subdivision into subgroups—for example, as in red deer and chickadees.

Since different degrees of tolerance are likely to exist between the members of a large group, any general increase of aggressiveness, whether expressed actively or merely by independence of action, may be expected to subdivide the group into corresponding subgroups. When a group has increased beyond a certain size, subdivision into subgroups may be followed by competition between these subgroups. An interesting parallel can be drawn between the dominance hierarchy within winter flocks of blue tits at a food hopper, where rank is related to individual aggressiveness, size (possibly), and distance to the center of a given individual's territory, and the similar hierarchy at a higher level of organization between family groups of gibbons, where rank has been related to the same criteria but applied to the group as the competing unit.

III. DENSITY AND SPREAD OF SPECIES POPULATIONS

Formal schemes dealing with the economy of animals have uniformly used density of the animals as the unit of measurement, emphasized the problem of overpopulation in relation to the capacity of the habitat, and proceeded from the assumption that the requirements for living and reproducing were met by random search for the necessary objects (cf. Nicholson, 1933). While such a random element undoubtedly exists, especially in the case of young, inexperienced animals, these theories must be modified, to a considerable de-

gree, in the vertebrates as a result of such manifestations of aggressive behavior as shown in territorial defense and in social hierarchies, and of tendencies toward the formation of aggregations. This later phase of the subject will not be discussed here (see Allee, 1931, 1938).

Random dispersal of the young, usually within limits of more or less suitable habitat types, has been described for many vertebrates. When the young are fairly well grown, they may wander off; active driving by the parents assists or stimulates this initial movement in some species (cf. Darling, 1937; Alverdes, 1935). The degree of toleration varies with the species, but the nomadic young are not infrequently harried from place to place until they find an open niche, often in a suboptimal habitat, or otherwise perish.

Restrictions of habitat, from whatever cause, such as are common on the periphery of a species' range, result in increased competition; and those animals unfortunate enough to be evicted from their territories here or elsewhere become nomads and receive the same aggressive treatment as is usual for the young until they become established again. A succession of favorable years may build up a relatively large density in peripheral habitats; later, severe restrictions of living conditions may force emigration from the area and may result even in the irruptive type of emigration. Quail are most likely to undergo violent fluctuations on the borders of their range (Leopold, 1933). Carrying capacity of a given area itself may depend, in good part, on the degree of social tolerance of the particular individuals which compose the group of quail which occupies an area (Errington, 1941).

Defense of territories is an important factor making for population stability in the case of many vertebrates. Predators, such as the territorial horned owl, resident in areas with alternative and abundant species of prey, may at times be self-limited and maintain relatively stable numbers (Errington, Hamerstrom, and Hamerstrom, 1940). Territorial size is readily compressible in the ruffed grouse (Clarke, 1936), which undergoes cyclic fluctuations in density. In birds the ease of compression of territories varies considerably with the species (Nice, 1941), as well as with population density (Kendeigh, 1941; Palmer, 1941); and such differences in tolerance may eventually help explain, to some extent, the nature of the population fluctuations which are exhibited. There is a possibility (cf. Nice, 1941) that intraspecies aggression, whether of a territorial nature or otherwise, by providing increasingly great resistance to crowding, helps cut down the incidence of disease and therefore the intensity of cyclic fluctuations which, in their more extreme form, appear to be a rather wasteful method of regulating numbers.

In addition to forcing diffusion of the excess population into suboptimal habitats, intraspecies aggression, which increases with crowding, may exert a regulatory action on population size by causing mortality directly. Field voles are territorial and, unlike Crew and Mirskaia's (1931) mice, will often fight to the death when crowded. In describing the results of an investigation of cycles in voles, mice, and lemmings Elton states (1942, p. 205) that

> this social antagonism among voles probably exists in nature and may be very important at different levels of population and may prove to explain some of the mortality at higher numbers. . . . ; we can see that there are inherent properties of the population dynamics of voles that may eventually explain their cycle as a self-contained system that is not so much dependent on other animals like predators and parasites as we at first supposed.

Cannibalism of the young by older, larger individuals is common in aggregations of young black bass (Langlois, 1937) and has been described for various other vertebrates (McAtee, 1936). Under certain conditions, many male carnivorous mammals will kill and eat the young (Alverdes, 1935). Mortality in nature due directly to social antagonism has been observed for tern colonies (Palmer, 1941), red deer (Darling, 1937), and muskrats (Errington, 1939*a*). Summer muskrats have few wounds, in contrast with the chew-up, wandering, and ill-situated muskrats of the late-fall and early-winter period of population readjustment.

Intraspecific strife may also stimulate the spread of a species into new geographic areas. Movement over suboptimal barriers into more favorable regions may be related to the territorial habit, as has been suggested by Burt (1940) for certain rodents.

A frequent consequence of the increased mobility at higher densities appears to be some reshuffling of the membership of local groups; this may take place about a nucleus of older residents, as in the case of bobwhite quail (Errington, 1941) and blue tits (Colquhoun, 1942). This reshuffling is characteristic of the period of population readjustment that follows the breeding season. It seems probable that a more rigid social organization exists within societies at lower densities of the species population above, and it may well be that this would facilitate survival in the species as a whole. Recent studies by Allee and Guhl (1942) indicate that in organized flocks of hens, as compared with groups kept in a state of social disorganization by a shifting membership, the average individual usually gets more to eat and gains more, or loses less, in body weight.

The existence of well-integrated societies requires a minimal number of individuals, and decrease in population density beyond a certain point may act to weaken social integration rather than to strengthen it. The importance of the problem of underpopulation in regulation of density has generally been underestimated (Allee, 1931, 1938). In a number of species this phenomenon is clearly related to aggressive behavior. Reproductive success is said to be relatively poor in small tern colonies because only a large colony can form an excited mob sufficient to frighten away the marauding gulls from the eggs of the terns (Stresemann, 1928; cf. Darling, 1938). When local numbers of American antelope fall below a critical level, the antelope fail to stand their ground or to bunch into a defensive formation which enables the bucks to fight off predators when the need arises—instead, they stampede and scatter, so that weak individuals fall an easy prey to their enemies (Leopold, 1933, p. 86). A similar phenomenon has been noted for certain other ungulates (Alverdes, 1935).

IV. RELATION OF AGGRESSIVE BEHAVIOR TO ANIMAL COMMUNITIES

Animal communities, like human communities, consist of progressively subordinated units. The role of aggressive behavior at the level of the individual, social group, and species has been suggested. It remains to discuss the relationship of aggressive behavior to the balance of density ratios of different species, in the relationship commonly known as the "web of life." The term "aggressive behavior" as used in this paper should not be confused with the idea of ecological aggressiveness, which is sometimes a synonym for high ability of a species to spread into new areas or to maintain position in regions already

occupied, and with which, like the various concepts of ecological dominance (cf. Clements and Shelford, 1939), this article is not directly concerned.

Interspecies competition may take the form of a direct attack of one species upon another, as in the oft-cited case of the English sparrow versus the bluebird and purple martin. Another case is that of the lizards, *Lacerta agilis* and *L. vivipara*, of Germany (Hesse, Allee, and Schmidt, 1937, p. 93). The former eats the young of *vivipara*, which is able to maintain itself only in regions where *agilis* cannot live. When the discrepancy in size of two competing species is very great, the smaller may simply avoid the larger species, making no attempt at physical combat, as in the case of bobwhite quail versus the ring-necked pheasant (Errington, 1941).

There is evidence that aggressive competition may be more intense within species than between species, and between kindred species to the extent to which they compete for similar objects than between species which are not closely equivalent ecologically. Gibbons will feed contentedly in the same tree with macaques and langurs, but they will not tolerate the presence of another gibbon group of the same species (Carpenter, 1940). Howard (1920) has summarized many cases of interspecific strife in birds. Some birds, like the moor hen, will attack almost any species of bird, not too large, which approaches their territories; but, in general, strife appears to be greatest between kindred forms and often involves competitors for nest sites or territory—for example, in birds of prey, in the tit family, and in woodpeckers. When not breeding, these birds sometimes travel in loose flocks made up of different species.

Competition by threat or physical combat is, of course, only one form of interspecific competition. Examples of other special forms of competition include reaction on plant habitat by competing animals and the phenomena associated with overlapping search, as in the case of the entomophagous parasite-host or predator-prey relations.

Psychological and Physiological Mechanisms of Aggressive Behavior

I. psychological mechanisms

The situations that lead to aggressive behavior in groups of children (Durbin and Bowlby, 1939) and in subhuman vertebrates seem to be fundamentally the same: the intrusion of strangers, possession of some object, and frustration. Punishment may be handed down to subordinates, as in chimpanzees (Yerkes and Yerkes, 1935) and blue tits (Colquhoun, 1942); and perhaps this can be looked upon as an example of the last category. Male *Platypoecilus* (Braddock, 1942) and male rhesus monkeys (Carpenter, 1942*a*), if frustrated in their attempts at copulation, may punish the female.

The term "aggressive behavior" denotes a complex phenomenon which may be partially broken down into simpler but overlapping stimulus-response components, as has been done to some extent by Lack (1939*a*) for the robin redbreast's territorial-defense reactions. The external situation seems partially separable into a flying-away movement, eliciting pursuit flight; robin shape, eliciting striking; a red breast, eliciting posturing; and song, eliciting song. Occasionally a robin will posture at a stuffed specimen lacking a red breast, or strike at a red breast, or sing at a silent robin. Secondary inhibition of the attack is well seen in the case of the female mate who has

all of the features normally eliciting attack but is, nevertheless, not attacked.

Aggressive-submissive behavior may be innate at times or in part, since chickens raised in complete isolation will attack a straw or hand extended into their cage and exhibit both fear and attack reactions when first exposed to normal chickens of the same age (Brückner, 1933). One phase of the problem involves, therefore, an analysis of the perceptive key stimuli which stimulate these apparently inborn reactions. Further analysis can be extended to conditioned stimuli and responses. In the terminology of Klüver (1936) the problem is to determine the degree or range of excitatory equivalence of a variety of stimulus situations and, similarly, of non-equivalent (nonexcitatory) situations.

No completely satisfactory studies of this type appear to have been made with reference to aggressive behavior. Apparently optimal and simple stimuli for a wide variety of instinctive responses, including attack reactions, of jackdaws have been described, by Lorenz (1931, 1935), in rather rigid fashion, as the specific releasers of these reactions. The matter is probably not so simple, since the optimum external stimulus situation may consist of a summation of several stimuli which in practice may often be separated from each other. For example, in the case of white leghorn cocks, the sight of a small, strange male in the home pen approaching the females with raised hackles is very effective in inducing an attack. It is readily conceivable that entirely different combinations of various stimuli, other things being equal, might produce the same intensity of response.

It seems doubtful if the details of a vigorous and active combat can readily be segregated into mechanical stimulus-response chains. A skilful, experienced combatant may anticipate the movements of an opponent. Studies of time relations of movements in films of animal fights have led to the belief that in such instances it is not possible to separate "stimulus" and "response" (cf. Klüver, 1936)—at least not in any immediate sense. Furthermore, different responses may be given to the same external stimulus, varying, for example, with the endocrine cycle, experience, fatigue, and fear. The motor response itself may change the nature of the external situation. The important thing is that the responses are co-ordinated and directed.

Another problem is to determine the influence of experience on aggressive reactions. Inhibition of the attack reaction may be based on acquaintanceship or other experience, as well as on subordination. Chickens may attack any strange chicken, whereas attacks on flock-mates are generally confined to relatively mild pecks. Even these pecks may be withheld if the subordinate abruptly ceases all movement. A large component of fear or attack reactions undoubtedly relates to conditioned behavior. This has been best shown in mice. It is interesting that it is easier to condition mice to become less aggressive by successive losses than it is to train them to be more aggressive by a series of wins permitted by matching them against submissive mice (Ginsburg and Allee, 1942). There is some evidence which indicates that experience in winning or losing may also be of some importance in deciding the outcome of paired initial encounters between domestic hens (Collias, 1944).

The various psychological correlates of aggressive behavior need more attention, as they frequently help throw light on the role which aggressive behavior plays in the life of an animal. Rats selectively bred for fearlessness in a

strange situation have been found also to be more aggressive in encounters with other rats and to be more susceptible to convulsive seizures when stimulated by an air blast. The converse was true of another strain (Hall and Klein, 1942). Careful genetic analysis is needed in order to find how consistent this association of different forms of behavior will prove to be.

II. PHYSIOLOGICAL MECHANISMS

The physiological factors responsible for aggressive motivation or for its inhibition have come to be somewhat better understood in recent years. These factors may be divided for convenient treatment into chemical or hormonal factors, characterized by relatively slow and sustained action on the intensity of a given drive, and into neural factors, which are responsible for the motor patterns of emotional and social expression. These two groups of factors are associated with hunger, fear, anger, sex drive, parental, and other social motivation or behavior.

CHEMICAL OR HORMONAL FACTORS

Strong hunger inhibits fear to some extent, and the animal becomes more aggressive. The specific physiological details of the mechanisms by which hunger influences aggressiveness do not seem to be known. In some cases, as in aggressive food competition between very immature animals, these mechanisms are clearly not associated with sex drive. After an extended analysis of hunger mechanisms, Carlson (1916, p. 230) concluded that

> the gastric hunger mechanism is primarily automatic or independent of blood changes as well as of central nervous influences; but in the normal individual chemical changes of blood as well as nervous impulses from the brain and spinal cord augment or decrease this primary automatism in a way to correlate it with the needs of the organism.

Blood from starving animals transfused into normal animals acts as a temporary stimulus to the hunger contractions of the stomach, and this indicates that chemicals carried in the blood stream play a role in the normal hunger mechanism. The influence of such blood changes on aggressive behavior represents a problem for investigation.

Inanition may exert indirect, as well as direct, influences on aggressiveness, as by lowering sex and parental drives. This may result in decreased tolerance and increased aggressiveness with respect to the mate or the young. These effects may be due in part to decreased secretion of sex and parental hormones and possibly to decreased sensitivity of the nervous system to these hormones. Severe inanition, by lowering male-hormone secretion, would act to decrease an important source of aggressiveness, especially against male rivals. This again appears to be primarily an indirect effect due to decrease in the gonad-stimulating powers of the anterior pituitary, as in rats (cf. Moore, 1939).

Sex or parental behavior in some species may be extremely resistant to food deprivation—for example, in breeding male fur seals and in broody hens, respectively. These animals store considerable food in the body and then eat very little. On the other hand, the physiological changes incurred in the normal life-cycle of an animal will influence the amount of food needed at any given period and, in case of a shortage, may largely determine the amount of competition for food at any given period.

In cats it has been demonstrated that increased secretion of adrenalin occurs concomitantly with fighting or flight reactions and with expressions of pain, fear, or rage. Adrenalin speeds up the heart rate, counteracts the effects of muscular fatigue, hastens blood coagula-

tion, and induces a number of other physiological changes which presumably would be of use to an animal in an emergency (Cannon, 1929). Allee and Collias (1938) were not able to change the social position or aggressiveness in initial paired encounters of normal hens by injecting them with adrenalin. Fear and rage as states of emotion have profound energizing effects on bodily activity, but bodily activity does not necessarily indicate subjective feeling. Human subjects injected with adrenalin, although manifesting the usual internal and external objective signs of strong emotion, generally deny that they really feel such emotion (Cannon, 1929, p. 356).

The difference in aggressive behavior of male and female is partly explainable by differences in sex hormones. Removal of the testis results in considerable reduction of aggressiveness of cocks (Domm, 1939). Uhrich (1938) found that castration diminished the fighting reactions of some, but not all, male mice. Decline in aggressiveness with castration may be slow, especially in some species.

Male pugnacity is probably not completely dependent on male hormone from the gonads; this is more true of some species than of others. Castrated male swordtail fish (*Xiphophorus*) are said to maintain their social position from 1 to 6½ months after castration (Noble and Borne, 1940). Dewlap display, flattening of sides and fierce fighting with teeth, precisely like bluffing and fighting of normal males, has been observed between male lizards (*Anolis carolinensis*) that had been totally castrated for 1 to 9 months (Evans, 1936*b*), although, as in males of the common domestic fowl, castration of male *Anolis* leads to a considerable reduction in aggressiveness (B. Greenberg, personal communication). Two hypophysectomized pigeons, when crowded together, have been observed to fight vigorously for 5 minutes with their wings and beaks after a postoperative period of over a year, but they did not bow or coo at each other in a formal way as normal pigeons may do.[3,4] The formal type of combat persisted for several months after hypophysectomy. It must be noted that, while the operation was performed by an expert, no direct check has been made of the completeness of removal of the hypophysis.

Treatment with androgens stimulates aggressive behavior in many vertebrates. These include: spayed and normal females of the swordtail fish, *Xiphophorus helleri* (Noble and Borne, 1940); both sexes of the lizard, *Anolis carolinensis* (Noble and Greenberg, 1941*a*, *b*); the turtle, *Chrysemys picta* (Evans, 1940); domestic hens (Allee, Collias, and Lutherman, 1939); male chicks of the domestic fowl (Noble and Zitrin, 1942); immature male and female black-crowned night herons (Noble and Wurm, 1940); female canaries (Shoemaker, 1939*b*); female ring doves (Bennett, 1940); female rats (Ball, 1939); and young boys, in the sense of increased independency (Bize and Moricard, 1937).

Few morphological effects of sex hormones are so consistent in the vertebrate series as is this stimulation of aggressive behavior by androgens. The increase in pugnacity was induced in both males and females, though not necessarily to the same extent. It involved rise in the social hierarchy in the case of the fish, turtle, domestic hen, and ring dove; however, such changes are not universal, since Emlen and Lorenz (1942) found only an increase in pugnacity of androgen treated birds and no observed change in the intraflock peck-order in valley quail. It involved stimulation of territorial de-

[4] I appreciate the kindness of Dr. J. P. Schooley, who hypophysectomized these pigeons for me.

fense in the night heron; and perhaps the reactions in lizard, canary, and ring dove are also to be considered as being predominantly of this type. Formalized combat (bowing and cooing), such as pigeons often use in defense of territory, was stimulated in an hypophysectomized male pigeon by treatment with testosterone propionate.[2] Singing is often used by small male passerines to advertise territory and warn off other males; it was induced in female canaries with this same potent androgen by Shoemaker (1939*b*). A high level of male-hormone secretion may induce a tolerance for or deference to females, since the male outside the breeding season soon loses such tolerance and becomes more aggressive toward females. Prolonged treatment of a hen with high doses of testosterone propionate will induce her to call other hens to food as a cock would do (Allee, Collias, and Lutherman, 1939) much more frequently than normally occurs.

Estrogens, in so far as tested, seem to have no effect or an inhibiting effect on aggressiveness. Female swordtails are said to have maintained their positions in the social hierarchy from 1 to 3 months after gonadectomy (Noble and Borne, 1940), and treatment of operated or intact females with estradiol dipropionate did not change social position. Removal of the ovaries from female lizards (*Anolis carolinensis*) results in increased aggressiveness and the urge to defend territory (Evans, 1936*b*). Aggressive behavior can be markedly inhibited in females of this species by treatment with estradiol dipropionate (Noble and Greenberg, 1941*b*). Removal of the ovaries results in decreased aggressiveness and decline in the social hierarchy among domestic fowl (Allee, Collias, and Lutherman, 1939). Treatment of female fowl with estradiol benzoate had no effect, or a depressing effect (depending on dosage), on social position or on success in initial paired encounters with untreated hens (Allee and Collias, 1940). Normal hens secrete both male and female hormone from the ovary, and presumably it is male hormone that is responsible for the normal level of aggressiveness.

It is possible that sex invitation by the female is to be considered in part as submissive behavior, and this behavior pattern is stimulated by female hormone in many vertebrates (E. Allen, 1939; Young, 1941; Noble and Greenberg, 1941*b*). Mounting, which is part of the normal oestrus behavior pattern in some female mammals (Young, 1941), may be induced by estrogen, progesterone, or androgen in female guinea pigs (Young and Rundlett, 1939).

Stimulation of aggressive behavior by male hormone and its inhibition by female hormone are two important ways in which normal male dominance and female submission may have been secured. Sex hormones, acting in various ways, provide a common physiological basis in many cases, especially those of seasonal breeders, for sex differences in territorial behavior, mating behavior, voice, coloration, ornaments, or weapons. In flocks of domestic fowl consisting of experimentally produced intersexual males the most masculine birds were at the top and the least masculine at the bottom of the peck-order; rank coincided, in general with the degree of masculinity of plumage (Domm and Davis, 1941).

Sex merely defines two modalities of behavioral patterns, as well as of morphology and appearance; and either males or females may at times exhibit behavior typical of the opposite sex. This seems to be especially true of females. Secretion of male, as well as of female, hormone from the ovaries seems to be a widespread condition among

normal female birds (cf. Allee, Collias, and Lutherman, 1939) and may occur in females of other vertebrates. Quantitative differences in male hormone secreted probably account for a good part of the normal differences between individual hens in aggressiveness (Collias, 1943).

Masculine aggressiveness in females, if excessive, might hinder mating; but the experiments on fowl (Domm, 1939) and night heron (Noble and Wurm, 1940) indicate that normally the male bird probably secretes considerably more male hormone than does the female. Subordination by the more aggressive male may normally stimulate feminine behavior in response to male hormone in the black-crowned night heron, whereas estrogens tested were found to be ineffective. Even males of rats (Beach, 1942) and lizards (Noble and Greenberg, 1941*a*) treated with an androgen may exhibit feminine behavior in response to a more aggressive male.

Both sex and species differences in behavioral response to crystalline sex hormones have been uncovered in recent years. Male but not female valley quail showed a decided increase in pugnacity when treated with testosterone (Emlen and Lorenz, 1942). In some species the importance of psychological and extra-gonadal factors may outweigh the usual effects of sex hormones. Several normal male pigeons placed separately in the home cage of a hypophysectomized male pigeon submitted passively or after a brief struggle to the latter, which was definitely aggressive. Injections of either testosterone propionate or estradiol benzoate into two hypophysectomized male pigeons induced pair formation accompanied by cessation of attacks on the female mate, which in each case was a normal bird.[2]

The relationship of other hormones to aggressive behavior has not been very thoroughly investigated. Gonadotropin from the pituitary probably exerts much, if not all, of its action on aggressiveness through the gonads. The adrenal cortex secretes certain androgens in small amounts; whether these types of androgen and in the amounts secreted normally stimulate aggressiveness to any important degree is not known. Thyroid extract increases pugnacity and speed of territorial defense reactions in the poikilothermal lizards (Evans and Clapp, 1940), but thyroxin injected in small amounts into normal hens was found to have no significant stimulating effect on success in initial encounters with strange hens or on social position, although in higher doses it caused molting, debilitation, inhibition of the gonads, and decreased aggressiveness (Allee, Collias, and Beeman, 1940). Birds generally retire into dense cover during the height of normal molt, or their territorial defense decreases considerably (cf. Nice, 1937).

Prolactin is of general occurrence in the anterior pituitary of vertebrates; and this hormone has been found to stimulate parental behavior in fish, chickens, and rats and markedly to inhibit gonadal activity in birds (Riddle and Bates, 1939). Defense of the young is an important aspect of vertebrate parental behavior. The young themselves have been shown to stimulate prolactin secretion in the parents in rats (Turner, 1939). The fact that prepubertally hypophysectomized young mice may be induced to display some degree of maternal behavior by putting suckling young with them (cf. Stone, 1939) indicates that extra-hypophyseal factors, perhaps in the central nervous system, are also of basic physiological importance.

NEURAL FACTORS

The neural mechanisms which directly or indirectly influence aggressive behavior act normally in connection with the hormonal influences, but for convenience in presentation they are treated as a separate unit.

The brain mechanisms responsible for co-ordination of the motor patterns of aggressive behavior appear to be in the lower brain levels. Forebrainless jewel fish, swordtails, and fighting fish (Noble and Borne, 1941), almost completely decerebrated pigeons (Rogers, 1922), and decerebrate cats (Bard, 1942) show co-ordinated, vigorous fighting; but adjustment of these patterns to specific social situations is markedly defective, especially as shown by inability to inhibit attack on other individuals. Cats with the brain removed or sectioned in front of (but not behind) the hypothalamus display a well-co-ordinated pattern of aggressive behavior or "sham rage" on the slightest provocation. Fear and rage centers have been demonstrated in the hypothalamus of cats by precisely localized electrical stimulation (Ectors, Brookens, and Gerard, 1938). Somatic and autonomic responses parallel each other in latency and intensity, suggesting that they are integrated in the hypothalamus into one or another functional system. Part of the physiological changes accompanying strong emotion are due to direct discharge over the sympathetic nervous system, which produces an effect quite similar to that of adrenalin (Cannon, 1929).

The neural mechanisms responsible for proper adjustment of the motor patterns of aggressive behavior into the social environment lie at higher brain levels (Gerard, 1942). Swordtail fish (*Xiphophorus helleri*) with deep lesions in the caudal half of the corpus striatum and decorticate cats apparently are not able to maintain the dominance-subordination hierarchy (Noble, 1939). This hierarchy depends on learning, and probably on other functions of higher brain centers as well, such as ability to control aggressive impulses and ability to comprehend a social situation. As is well known, the general cerebral cortex of mammals is of primary importance in the formation of habits, but subcortical brain levels may also play some part in this even in these animals (Marquis, 1940). Forebrainless cichlid fish can learn to know new nesting territories and mates (Noble, 1936).

On the basis of the excessive and sensitive rage reactions of decerebrate cats Bard (1934) has suggested that one normal function of the cerebral cortex is to inhibit excessive aggressiveness in mammals. Hyperaggressiveness in operated cats declines somewhat with time, and the possibility does not seem to have been entirely excluded that an irritation effect may play a role in such hypersensitivity (cf. Bard, 1934; Marquis, 1940). The cerebral cortex is usually considered to be the most sensitive part of the brain to oxygen lack, and some support to the inhibition theory is provided by the effects on human behavior of acute anoxia at high altitudes. Simulation of such conditions on subjects in decompression chambers may lead to explosive emotional outbursts with periods of laughter, anger, or pugnaciousness (Armstrong, 1939, p. 276).

Difficulties of comprehension may play an important role in the inability of animals to maintain a dominance hierarchy after certain brain operations, especially such operations as produce symptoms similar to those of visual agnosia in man. Klüver and Bucy (1939) found a very considerable decrease of motor and vocal signs of anger and fear in monkeys —animals which normally depend to a

high degree on visual stimuli—after removal of the temporal lobes of the brain. Such monkeys, judging from the results of various tests, have little difficulty in discrimination of elementary visual stimuli but appear to be "psychically blind"; and the essential difficulty does not improve much with time. They may bite each other, but fights never develop. After being attacked and bitten by a normal animal, such a monkey may approach this animal again and again in an attempt to examine it. On the other hand, these authors, on the basis of previous experiments (see their earlier papers), doubt that a monkey would be seriously hampered under natural conditions, in the wild, by a loss of its prefrontal region, its parietal lobes or its occipital lobes, as long as small portions of the striate cortex remained intact.

The precise relations of the hypothalamus to other parts of the brain are of interest, since it appears to be an important center for motor co-ordination of aggressive behavior, at least in mammals. Such relations may be established by anatomical connections and by intercellular electric currents (Gerard, 1941). Many of the significant interconnecting anatomical pathways have been suggested recently by Papez (1937) in relation to a proposed theory of the mechanism of emotion. These pathways link the hypothalamus more or less directly with the other levels of the brain, as well as with the pituitary gland. Their relationship to aggressive behavior, anger, and fear requires further investigation.

There is little or no evidence that the hypothalamus governs or even mediates emotional experience (Lashley, 1938; Masserman, 1943). Recent opinion inclines to the view that the cerebral cortex, rather than the hypothalamus, is the center of subjective emotion, as contrasted with the expression of emotion (Lund, 1939). The high cortical development of man adds emotional tone to the most varied incidents and makes possible extremes of nobility and of depravity not accessible to the lower animals. The psychiatrist tells us that the results of excessive domination or submission are everywhere present in the psychopathic hospital (Myerson, 1936).

Genetics of Aggressive Behavior

Not much work has yet been done on the genetic analysis of aggressive behavior. A large part of the differences between individuals, races, or species in aggressive behavior, and to a lesser extent in such accessories as color characters used in threat display, may be nonhereditary and a result of differences in circumstances or environment. But genetic differences have also been demonstrated. J. P. Scott (1942) and Ginsburg and Allee (1942) found differences in aggressiveness of three different laboratory strains of mice. By selective breeding (for another goal) it has been found possible to separate from the original common stock two different strains of rats, in one of which the individuals are very aggressive in encounters with other rats while in the other the reverse holds true. Individual differences in aggressiveness appeared to be fairly stable and consistent (Hall and Klein, 1942).[5]

Presumably differences in a complex and graded character like aggressive behavior are generally affected by many genes, but the matter needs experimental analysis. Not merely the number of different genes but the organization of gene systems must form the important basis for differences in aggressive behavior. The proportional importance of hormones and the central nervous system

[5] Keeler (1942) has presented evidence that the black (nonagouti) gene in the Norway rat is associated with lesser aggressiveness, in the sense of tameness. However, the term "aggressiveness" is used in a different sense in this paper.

in determining degree of aggressiveness varies greatly in different species. This means that different combinations of genes may be responsible in different species for the same degree of aggressive behavior. In the case of color characters the genetic differences vary from simple to complex. A relatively simple case is that of the blue-winged and golden-winged warblers, where the difference appears to depend on two major dominant factors (Morse, 1926) and, judging from the degree of intergradation, on a number of minor modifying factors.

Relation of Aggressive Behavior to Evolution

I. Relation to factors of evolutionary change

From the point of view of the early stages of adaptive evolution the more interesting effect of competition is the survival of the more fit and not the survival of the more fortunate individuals. Studies of the statistical transformation of populations in nature, especially at critical periods, in relation to the behavioral and other adaptive characteristics of individuals are needed in this connection. It has been observed that injured, immature, and ill-situated animals are generally subject to increased mortality or decreased reproduction. More discriminating data, while not altogether lacking, are scarce. Some of the evidence which has been reviewed with respect to aggressive competition seems to be pertinent and may provide suggestive leads.

Certain illustrations can be given of early stages in the evolution of species differences in aggressive behavior in which one factor of evolution—for example, isolation or selection—appears to dominate the picture.

Divergence with isolation, as of local populations, races, or species, may occur in the absence of environmental differences or of any evident correlation with such differences. The role of selection would appear to be minimized; and presumably such divergence is due to the random effects of local inbreeding (Wright, 1931, 1932, 1940), as well as to the more or less random nature of the foundation stock. The major difference in the breeding habits of the eastern and western races of the black-nosed dace is that the sexually ripe males of the latter race show a greater tendency to establish and hold territory in which they breed. In contrast, the breeding males of the eastern race may defend a territory for a short time against other males; but, when a female comes near, they desert the territory to spawn at any spot in which they succeed in cornering her (Raney, 1940).

Eastern and western races of the wood peewee differ in their territorial songs, as do eastern and western species of the meadowlark. The latter may occupy the same areas at the juncture of their ranges without forming an intergrading population and so represent a terminal stage in the process of speciation. More extensive overlapping of range is seen in the case of the red-winged blackbird (*Agelaius phoeniceus*) and the very similar tricolored red-wing (*A. tricolor*). Both nest in similar, sometimes in the same, marshes; but the latter is much more colonial, and its territorial song, fighting, and threat display are feebler (Lack and Emlen, 1939). The former is divided into more than a dozen different races spread over the country, but the tricolored red-wing is monotypic and largely confined to Oregon and California.

Aggressive behavior is an important organizing force in social and community integration of many vertebrates, and selection has drawn on it to determine a specific set of adaptive reactions, just

as selection has operated on cell reactions in relation to individual organization. Some idea of adjustments to environmental stress within the species limit may be drawn from a study of the basis of covey size in bobwhite quail. These birds are especially subject to winter starvation and losses from very cold weather in the northern parts of their range (Leopold, 1933). During severe winters the birds in whole counties may be wiped out. Quail huddle together under stress of cold, and in a laboratory analysis Gerstell (1939) found that within limits the temperature of the group and the survival rate were directly proportional to the size of the group. Quail coveys keep down their own size by aggressive behavior (Errington, 1941) within the usual limits of 10–30 birds, which appears to be the number that can roost together comfortably in the characteristic circle with heads facing out (Errington and Hamerstrom, 1936). Isolated birds may be excluded from the covey, and their greater mortality agrees well with Gerstell's findings. Interestingly enough, the average covey size of 1,100 flocks of bobwhite was found to be larger (12.5) in the north-central states and smaller (10.5) in the Gulf states (Wing, 1941). It is apparently unknown whether this difference has any genetic basis; it clearly has survival value. It is possible (cf. Errington, 1941) that this adjustment is not based on genetic differences and therefore does not represent true organic evolution, if by the latter is meant some shift in gene frequency of a natural population (Wright, 1931). This phenomenon in quail is a social application of Bergmann's rule that among homoiothermal animals the same or related species attain a larger size in colder than in warmer regions (Hesse, Allee, and Schmidt, 1937, p. 386).

Relaxation of selection pressure results in the decline and loss of territorial defense reactions in the more parasitic species of cowbirds and in the decline and loss of secondary sex plumage in the various species of Galapagos finches (Swarth, 1934). The causes of degeneration are to be found in the random effects on organization (of a complex pattern of habit, color, etc.) of mutation pressure or of local inbreeding; it is also possible that selection for some other character might be exerting an indirect and deleterious influence on a given character freed from selection pressure (Wright, 1940).

Aggressive behavior is selected with reference to its influence on different levels of organization. It should be noted that Darwin (1859; 6th ed., 1872, p. 52) used the term "struggle for existence" to include not only the life of the individual but success in leaving progeny. That there need be no ambiguity here becomes clear when we consider that two different levels of selection are involved—that of the individual and that of the group. Such considerations lead to the recognition of important relations between aggressive behavior and competition, on the one hand, and co-operation, on the other; and these relations have real evolutionary significance both for the evolving individual and for the evolving social unit.

Aggressive behavior may serve as an important social mechanism in many vertebrates; and integration at one level of organization is based, in good part, on integration at lower levels, just as the proper functioning of an individual animal depends on the proper working of its organs, tissues, and cells. It has not been sufficiently recognized that competition at one level of organization may be regarded as co-operation at another level. Competition between individuals for

food would seem to be the most egocentric type of competition, but from the point of view of the family it means that the animals which become parents are likely to be those which are most efficient in securing food for their progeny. Close competition may lead to a considerable individual increase in food intake as compared to more isolated animals, as has been experimentally demonstrated in chickens (Bayer, 1929) and other vertebrates; and presumably this might facilitate the development of social life apart from any necessary connection with the family. Competition between individuals for mates is co-operation in the sense that the formation of the most vigorous and synchronized sex pairs is favored. Competition between sex pairs or family groups, such as those of geese and gibbons, is co-operation from the viewpoint of subspecies or other major subdivisions of the species, in the sense that the more prolific the family groups the greater the local emigration from a particular subpopulation is likely to be. This leads to competition between the subgroups, with dispersal tending to equilibrate the population at the points of dispersal. The effective invaders interbreed with or replace the rest of the species and so tend to tone up the whole species (cf. Wright, 1932). This process can be considered as co-operation from the viewpoint of the species. Competition between species and even the predator-prey and plant-herbivore relationship can be looked upon as co-operative processes in the exploitation of the energy resources of the inanimate environment by the community. The data of paleontology tell us that predator and prey pace each other in an evolution toward reciprocal adaptations, and this principle can be extended throughout the animal community wherever species are subject to opposed selection pressures. Since this results in a moving equilibrium, we are led to the principle of community evolution, with excessive emigration leading to the spread of the communities best fitted to the environment.

Increased competition at one level may therefore mean increased co-operation at a higher level of organization, which in turn means increased efficiency in intergroup competition at this higher level. Similarly, increased co-operation at the lowest levels may lead to increased efficiency in intergroup competition at higher levels, and the relationship just outlined is repeated. Competition and co-operation are each exerting such influences at every level of selection. Individuals are very often selected in terms of *social* values; and competition, provided it does not become excessive, is very often desirable from a social point of view. Groups seem to be the usual units of selection. This latter conclusion has been reached in somewhat different ways by Allee (1931, 1938, 1942), Wright (1931, 1932, 1940), Emerson (1939), and Thomas Park (1941).

Allee (1938, 1940, 1941, 1943), Emerson (1939), and Gerard (1940) have emphasized the co-operative relationships of animals in recent reviews. The many parallelisms and analogies which the latter two authors point out for insect and human societies, when compared with the organization of individual animals, including man, serve to bring out the point that selection has operated toward a similar end in both cases. The extensive convergence means that societies can be considered the biological servants of their component individuals, in the same sense that individuals could be looked upon as servants of their component cells.

Aggressive behavior is, of course, only part of a complex of many characters subject to selection at any particular

level of organization. Aggressive behavior may be reduced, may be enhanced, or may assume special forms of expression according to the nature of associated organizing and integrating factors. For example, adjustment to cold weather by quail favors social tolerance over aggressiveness; the parasitic habit in cowbirds removes much of the value of territorial defense for them; development of co-operative group aggressiveness may replace the need for individual aggressiveness to a considerable extent; advantages apparently incompatible with excessive aggressiveness, such as the prevention of undue fatigue, may lead to a compromise like threatening, bluffing, or formal combat; while other characteristics may be preadapted to the service or control of aggressive behavior, such as the cerebral cortex in higher mammals.

II. EVOLUTIONARY TRENDS IN AGGRESSIVE BEHAVIOR AND RELATED SOCIAL PHENOMENA

Certain major trends of evolution related to aggressive behavior can be described. These trends are probably just as complex and ramifying in their effects as any influence on the integration of the animal community is likely to be; but, as yet, only the simpler or more obvious interrelationships can be followed with much assurance.

The origin of aggressive behavior is obscure. One possibility is that aggressive competition for food may have preceded aggressive competition in relation to reproduction. Cannibalism of smaller, especially of young, individuals is a widespread phenomenon in vertebrates (McAtee, 1936; Langlois, 1937). Groups of immature jewel fish (Noble, 1939) and immature black-crowned night herons in the nest (Noble, Wurm, and Schmidt, 1938) have a nip-order or a peck-order which is later disrupted by the development of the instinct to defend separate territories.

THE MATING RELATIONSHIP

There is a possibility that aggressive behavior among vertebrates may have arisen in evolution as a result of competition between males to fertilize eggs located in a definite place or nest. An interesting start is made even among the lowly cyclostomes. Sex recognition appears to require physical contact in the brook lamprey, which lays its eggs in nests. The lake lamprey is less social; it does not require physical contact for sex recognition, and the males are somewhat pugnacious; this has led to partial polygamy and the formation of incipient territories (Noble, 1938).

In the lake herring each female scatters her eggs widely; and, although several males may follow a female as she descends to the bottom to deposit her eggs, there is no fighting, nor is there any restricted territory (Noble, 1938). Many of the marine teleosts breed in large swarms, and the females lay an enormous number of eggs; the eggs, which are shed at intervals, float and are dispersed widely by currents. It would seem that there is comparatively small opportunity for selective fertilization, such as would be necessary to give much point to antagonistic competition between males for females. As a rule, however, the female has a male in close attendance, and more data on possible presence or absence of aggressive competition between males for females is desirable. Courtship is rare among marine fishes, but the male of the common dragonet (*Callionymus*) has a brilliant nuptial display and establishes close contact with the female; eggs and milt are extruded at the same moment, and the males attempt to frighten away rivals. No care is given to

the pelagic eggs or young (Norman, 1931).

In some fish in which the eggs are fertilized externally, they are grouped and hence provide more of a chance for selective fertilization by the males. Some marine fishes which breed in shallow water and many fresh-water fishes lay demersal eggs which commonly adhere in a mass on the bottom. Aggressive competition between males for females or territory is common; often the male builds a nest and guards the eggs (Norman, 1931).

Another way of making possible selective fertilization has been the method of internal fertilization. This is generally associated with terrestrial life, or among fishes with the bearing of live young, as in the case of many elasmobranch fishes and some teleosts. It may be worth noting that the elasmobranchs are relatively primitive among fish. In many of the rays the males have a patch of sharp spines on each pectoral fin above; and it is known that several males will pursue a female, fighting and buffeting each other with their fins (Norman, 1931, p. 295). The males of live-bearing teleosts, like the guppy and swordtail, are very pugnacious (Noble, 1938).

Aggressive competition, as observed in terrestrial vertebrates, may be keener in cases of polygyny or promiscuous polygyny than in cases of monogamy. In the sage grouse on its mating grounds J. W. Scott (1941, 1942) observed that 3 per cent of the males did 87 per cent of the mating. In the house wren, which as a rule is monogamous while raising a given brood, there are about 15 per cent more unmated males than females (Kendeigh, 1941). An intermediate example is that of ducks, which form their comparatively loose and temporary pairs while migrating in the spring flock. In blue-winged teals extensive data indicate that at this time there are ordinarily about 50 per cent more males than females; and each female may be attended by two or more competing males (Bennett, 1938). Lack of aggressiveness is associated with sexual promiscuity in certain fish (Noble, 1938), amphibians (Noble, 1931), most snakes (Noble, 1937), and certain bats (Alverdes, 1935).

In the case of polygyny, selection appears to emphasize the individual male; and there may be only a very loose limit to evolutionary trends in characteristics that aid aggressive competition for females. Increase in size of polygynous males of terrestrial vertebrates is a good example, with such extreme cases as that of the very pugnacious fur seal, in which the male may be from six to twelve times larger than the mature female. Large size, while perhaps not generally of primary importance within the species (Collias, 1943), except where size differences are extreme, has been found to favor high social position in certain laboratory groups of fish (Noble, 1938), turtles (Evans, 1940), lizards (Evans, 1936*a*), chickens (Schjelderup-Ebbe, 1922), mice (if differences are large enough, Ginsburg and Allee, 1942), and various primates (Maslow, 1940).

Sex differences in aggressiveness are connected with the type of mating system characteristic of a given species. In polygynous or promiscuous polygynous species the females tend to be relatively more social and in most cases fight much less than the males, if at all—for example, in viviparous fishes, red deer and other ungulates, and the fur seal. In the case of territorial polygyny in birds the females may defend small subterritories against each other within the larger territory of the male, as in the case of the corn bunting (Ryves and Ryves, 1934); such defense may be very lax and

occasional in some species, like the tricolored red-wing (Lack and Emlen, 1939). The female in many monogamous species is almost or quite as aggressive as the male—for example, in jewel fish (Noble and Curtis, 1939), in certain birds (Nice, 1941), and in gibbons (Carpenter, 1940). Defense of the mate against rivals in these cases is characteristic of both sexes, and the female may aid in the defense of the territory of the sex pair. In the few polyandrous birds, such as tinamous, button quail, painted snipe, and perhaps phalaropes, the female is the conspicuous displaying sex (Lack, 1939*c*); but precise and sufficient data on relative aggressiveness of the sexes in these species seems to be scarce. In the suggestive phalarope case the female is known to be very aggressive (Tinbergen, 1935).

The evolution of territorial defense among vertebrates has been closely associated with that of the mating relationship. While territory may at times be unconnected with reproduction, as in the case of roosting or winter territories of birds, in general it is especially associated with nests and eggs among vertebrates (Noble, 1939), at least in its more rigid aspects. Many fresh-water fish (Noble, 1938, Breder, 1936), many lizards (Noble and Bradley, 1933; Evans, 1938*a*, *b*), and the great majority of birds (Nice, 1941) furnish examples. Territorial defense is absent or relaxed in viviparous and school-breeding fish (Noble, 1938) and in the parasitic cowbirds (Nice, 1941), and during the nonbreeding season in fish, lizards, and birds in general. The functions of territorial defense in birds may be extended, specialized, or elaborated to subserve mating, nesting, and feeding uses, details of which have been summarized by Nice (1941). The great majority of mammals are viviparous; and their territorial defense does not seem to be very rigid, since there may be extensive overlapping between neighboring territories (Heape, 1931; Alverdes, 1935; Burt, 1940; Carpenter, 1934).

Territorial organization results in dispersion within populations. Wide dispersion of individuals within a species may be caused by a dispersed food supply and a need for increased safety from predators while breeding. Small land birds seem especially subject to these difficulties. Of some 67 living families of passerine or perching birds, gregarious breeding is found in only 9 (Friedmann, 1935). The presence of an abundant and concentrated food supply, together with relatively safe breeding places, makes possible gregarious breeding in most sea birds (Howard, 1920; Friedmann, 1935) and, for example, in the marine iguanas of the Galapagos (Schmidt, 1935), among other animals; and their individual territories are very small.

Increased formalization of combats is an example of an evolutionary trend apparently determined by opposed selection pressures. Formal combat by means of special display may in turn stimulate formal combat by the opponent. Adult male blackcocks will violently attack other males; but, if instead of running the latter displays, the attack promptly changes over to display fighting (Lack, 1939*b*). The presumed advantage is the avoidance of undue fatigue, and therefore conservation of energy for reproduction and increased safety from predators. The matter may be complicated by special factors in particular instances, but the general trend seems clear. In general, vertebrates bluff or threaten before they resort to fighting to settle conflicts, and a given individual will frequently not face an obviously superior foe.

Huxley (1934) has extended Hingston's (1933) views on the biological antagonism between threat coloration and concealing coloration to all characters whose function it is to make the organism less conspicuous and all whose function it is to make it more conspicuous. For example, even the male ruff (*Philomachus pugnax*) is a cryptic bird when its conspicuous ruff is folded. There are many cases among birds in which special characters or colors are developed only for use in the breeding season and which are employed only for intermittent display. During formal combat the body color of fish and lizards may become much brighter or darker; the loser quickly becomes dull or pale again, whereas the winner may remain bright for some time (Norman, 1931; Noble, 1938; Evans, 1938*a*).

Evidence has been presented for different species of fish (Noble, 1938) and especially for lizards (Noble and Bradley, 1933) that the greater the development of threat coloration and behavior the less does actual fighting occur. The same thing has been noted for birds (Selous, 1933). In the tiny blue tit, fighting is said to be entirely psychological (Colquhoun, 1942). This is what one might expect in small birds, since such birds have many enemies and would fall ready prey to a passing predator should they become very fatigued. However, active combat involving physical contact is not uncommon in its close relative, the black-capped chickadee (Hamerstrom, 1942).

The robin redbreast displays its conspicuous breast to frighten intruding robins off its territory. Other species of birds of approximate robin size and shape which display some red in their plumage seem especially prone to attack (Lack, 1939*a*). Such an attack on birds with a superficial resemblance to the species concerned, apparently without much regard for the biological usefulness of the attack, seems to be widespread among birds (cf. Lack, 1939*a*; Tinbergen, 1935; Davis, 1942).

Males, as a rule, are much more aggressive than females; and this is correlated with the occurrence of sex dichromatism in many species of fish, lizards, and birds. Noble (1938) has reviewed the case among fish. In most territory-guarding fish the males are conspicuously colored, and the females are conspicuous in species in which they defend the nest or young. The nuptial colors of the males of many viviparous fish may serve, in part at least, as a warning for other males to keep away. In most fish which breed in schools there is no sex dimorphism in color and little or no sex rivalry. In lizards and birds bright colors of the male also frequently seem to be displayed during defense of territory. In phalaropes the female vigorously defends territory and the male incubates alone; this reversal of normal sex relations is correlated with brighter, more conspicuous coloration of the female.

Most amphibians show little or no sexual dichromatism (Noble, 1931, p. 116), and aggressive behavior seems to be very poorly developed in the amphibians, aside from infant cannibalism. If two or more male wood frogs get a good hold on the same female, they try to dislodge each other by strong kicks of the hind legs (Banta, 1914); but no male frogs are known to fight with their teeth for the possession of a female (Noble, 1931, p. 125), despite the existence of sex differences in teeth of some forms. Noble (1931), who has summarized an extensive literature on the subject, states (p. 115) that

> in all Salientia where the courtship and mating has been adequately analyzed, sight has been found to play almost no part in sex recognition,

other than to inform the male of the approach of another object of suitable size or movement.

Sex dichromatism among snakes is rare and is correlated with fighting between males for the females, as in the European adder. Most snakes resemble amphibians in that sex recognition is effected largely by sensory modalities other than vision, and fighting between males for females appears to be uncommon (Noble, 1937). Sex dichromatism is not very common among mammals, and this fact is associated with their usually nocturnal habits or relatively large size.

There is no implication here that formal combat by males is the only factor responsible for sexual dichromatism. For example, while sexual dichromatism among birds is associated with vulnerability to predation (Mottram, 1915), this association may be due either to formalization of fighting tendencies or to need for inconspicuous coloration of the incubating sex or both. Among birds the less the male shares incubation and feeding of the young, the more he differs from the female with respect to conspicuous display characters (Huxley, 1930).

In species among which, because of nocturnal or skulking habits or other reasons, conspicuous coloration would be of limited usefulness, if not detrimental, the mode of fighting may be very vigorous, or else formal combat acts through other sensory channels than vision. *Ctenops vittatus*, a close relative of the fighting fish (*Betta*), as if to compensate for its somber tones, replaces the brilliant threat display of its relative by growling loudly as a challenge to passing females (Noble, 1938). The mode of fighting is quite vicious in nocturnal reptiles, such as geckos and alligators; and often fights end in the death of one of the combatants. The nocturnal geckos lack intimidating structures or bright colors, depending instead upon vocal signals (Evans, 1936*c*). However, Greenberg (1943) noted that in the peculiar western banded gecko of North America fighting is not very intense and voice does not enter directly into the fight pattern but is only heard when one of the geckos is bitten. Male house wrens, which are dull-colored birds and very similar to the female in appearance, largely compete for territory and females by means of vigorous singing contests (Kendeigh, 1941). Fighting may be vicious in mammals, many of which, while they have good vision, are more active by night. On the whole, most mammals seem to be comparatively inconspicuous in coloration. The use of threat sounds is widespread among mammals. About half the sounds made by wolves are said to express anger (Alverdes, 1935). Vocal combat may also be important in diurnal mammals. Battles between groups of howler monkeys are largely vocal, and this is often the case between family groups of gibbons (Carpenter, 1934, 1940).

The same display is used by males in threat and in courtship, as a rule, only in species of birds like the raven, in which the sexes appear alike; in such cases one function of the display is to serve as a method of sex diagnosis, since a male will depart or respond similarly and a fight may ensue, while a female will either depart or respond with behavior which may eventually lead to mating (Huxley, 1934). Aggressive behavior is also used as a method of sex diagnosis by males of some fish, like the red horse and hog sucker, in which the sexes appear alike (Noble, 1938). Courtship behavior may in part have originated as extraneous or substitute activity, presumably serving in a tension-releasing capacity for a highly emotional situation—for example, as when different drives con-

flict, such as the sex drive versus the urge to attack the approaching partner in a newly mated European blue heron (Tinbergen, 1939).

A complex and important evolutionary trend is that determined by dominance relations between the sexes of a mated pair. In the case of monogamous pairs, where both parents help in the care of eggs or young, the mated pair must maintain its stability for some time. Sex pairs have the strongest and most enduring bonds in those species of fish (Noble, 1938) and of birds (Huxley, 1930) in which there is most elaborate or reciprocal courtship. It is in such mated pairs that greatest tolerance, deference, or protection is given to the female by the male—for example, in pairs of night herons, geese, and canaries, as compared with the loose, temporary unions of sage grouse, red deer, and rhesus monkeys. The female out of oestrus or out of the breeding season may lose much of her attractiveness to the male, and the male may lose much of his tolerance or "chivalry" for the female. This would appear to place the female at a serious disadvantage in the struggle for existence, especially, in polygynous forms where the male is generally much larger and stronger than the female and often equipped with special weapons. But close competition is usually avoided, because such males, when not breeding, frequently keep apart from the females and young; and they may, especially in mammals, form unisexual male groups (Alverdes, 1935).

THE FAMILY

The family in vertebrates may have had its roots in the sex jealousy of males competing to fertilize eggs, since this was apparently followed in many fresh-water fishes by extension of the defense reactions of the male to include guarding of the fertilized eggs and young.

Since in all classes of vertebrates the male, as a rule, is the more aggressive sex, his sex jealousy is a more effective block to the prolonged extension of family ties than is that of the female. This difficulty has been circumvented in certain species, like the red deer, by excluding the male from the family group, except during the relatively brief mating period. In other species, like the promiscuous howler monkeys, the difficulty is met by apparently eliminating aggressive competition for females. In other species, as in the higher primates, the slow physical maturation of the young may be an important factor. The relatively less aggressive female plays a much more important family role in the higher, than in the lower, vertebrates. Among fish the female often merely lays the eggs over the spawning grounds or in the nest built and guarded by the male. In some species she may help guard the eggs, as in the jewel fish. Some female fish also have developed ovovivipary. In many amphibians the female may desert the eggs after laying, or she may stay near them and exhibit other types of parental care (Noble, 1931). Although some salientians exhibit close parental care of highly specialized kinds, all in all, there is little, if any, advance over the parental care shown by some fish. Female turtles often dig a burrow in which they bury their eggs. Many snakes are ovoviviparous (Ditmars, 1936), and different species of reptiles exhibit more advanced parental care. Among many birds it is the female that is most active in incubation of the eggs and care of the young, and in the viviparous mammals she usually takes the leading role in rearing her offspring.

In birds and mammals the young do not usually become independent as early as do the young of lower vertebrates, and they are cared for by their parents for a

longer period of time. There is a possibility that, accompanying the increase of parental care of young, there has been a decrease in the precocity of young with respect to the appearance of aggressive behavior. More data are needed to settle this point. Fighting behavior appears in the fish *Platypoecilus maculatus* almost from the day of birth (Braddock, personal communication), in chickens roughly from 3 weeks (males) to 3 months (females),[2] while the young of man are quite helpless and unaggressive for many months.

It has been suggested that the prolonged education and association of the young with their parents may be the important basis for the greater social development of the higher, as compared with the lower, primates (Yerkes and Yerkes, 1935). The higher social development of red deer, as compared with roe deer (Darling, 1937), and of jackdaws, as compared with most other birds (Friedmann, 1935), is also associated with much greater overlapping of generations and greater tolerance of one or both parents for the young, even after the latter are well grown. However, the capacity to train the young may be very limited in lower vertebrates. It may be remarked that increase in size of organized groups which facilitates social advance does not necessarily depend upon the extension of family ties.

ACQUAINTANCESHIP GROUPS

Judging from the examples which have been reviewed in the preceding pages, the degree of dominance exerted by a group of vertebrate animals depends on the numbers of individuals of which it is composed, on the size of individuals, on proximity to its territorial center, on degree of integration, and on general level of aggressiveness of its members.

The number included in a stable and organized group depends, in large part, on memory for individuals and probably tends to increase with rise in the vertebrate series. In the viviparous fish *P. maculatus*, groups as large as 4 fish are not usually able to maintain stable hierarchies for much longer than 1 or 2 days; and most groups of this size cannot maintain a straight-line hierarchy, although groups of 3 usually do so (Braddock, 1942). However, it has been stated that the related *Xiphophorus* can maintain stable hierarchies in groups of 4 for months (Noble and Borne, 1940). Flocks of domestic hens with less than 10 birds can maintain stable hierarchies for many months, and straight-line hierarchies are common. Stable, organized groups of various primates in the field may often be considerably larger and may have a high degree of constancy from season to season and even from year to year—a constancy which is affected by increments due to reproduction, maturation, and group splittings or additions (Carpenter, 1942*c*). Among laboratory mice the capacity to recognize individuals is apparently very poor (Ginsburg and Allee, 1942); Uhrich (1938) observed that albino mice caged in groups of generally 3–8 individuals would maintain a given social order from a few days to several months.

While more study with special reference to the problem is needed, co-operation in attack and defense reactions above the level of the sex pair seems to be rare, if it has been described at all, for fish or lizards in which the sex pairs are comparatively unstable. Co-operative defense of territories by stable, organized groups other than by a simple sex pair has been described for a number of birds and mammals.

The evolution of co-operative competition involving attack or defense by the group as a unit has been greatly

facilitated by such attractive forces as sex and parental drive; but often the competing unit has been increased by attraction of unrelated acquaintances, and it may even be based merely on acquaintanceship. Increasing tolerance within groups not only has operated to make possible increase in size of group but directly facilitates (and probably is facilitated by) development of co-operative defense reactions. In general, the sequence of development of highly social groups was probably as follows: (1) continual, individualistic fighting without formation of a stable hierarchy; (2) inhibition of domination behavior between subordinates by the group despot; (3) tolerance of aggressive behavior of subordinates (at first merely the mate); and (4) extension of such tolerance to the immediate vicinity of the despot—a tolerance which permits more or less simultaneous attack of strangers by both despots and subordinates. Such co-operative attacks would permit dominance over large and powerful strangers capable of easy victory in single combat; they would therefore be expected to be preserved by selection.

All this gives us some insight from a biological point of view as to why primitive groups of peoples have two codes of conduct—one of peace for fellow-members of the group, and usually one of aggression for strangers and other groups (Durbin and Bowlby, 1939). Aggressiveness in the sense of belligerence, is related to human warfare. The directness of this relationship is a matter of some conflict. It depends in large part on the definition used for war, and the matter is too complicated to be reviewed here. Different aspects of the subject are presented by Durbin and Bowlby (1939), Quincy Wright (1942), and Malinowski (1937). The fighting tendencies of man are based in part on the selection pressures that have played upon his ancestors, and an attempt has been made to clarify these selection pressures in the foregoing pages. Beyond the existence of leaders, sentinels, and the predominant roles of males in aggression by heterosexual groups, there does not appear to be much special organization for group defense in small, stable, organized groups of infrahuman vertebrates; and, except for the use of missile weapons, the most primitive groups of man do not appear to be very superior in this respect.

COMPOUND GROUPS

Groups compounded from smaller groups of the same species may react more or less as a unit. These groups are often of very large size; and the congregation of individuals is made possible by a concentrated food supply, by movement of the group from one feeding ground to another, as in the case of migratory flocks of birds, or by the group's scattering over a wide area while feeding, as in the case of many seabirds, jackdaws, rooks, red deer, and baboons, and coming together while breeding, sleeping, or if alarmed. These large groups, as a rule, are more or less open to newcomers, and the compound organization tends to be rather loose (Alverdes, 1927). Among baboons the leaders and sentinels are often the largest and strongest males; and, when danger threatens, they meet it with organized defense reactions as a group (Allee, 1931, p. 349).

Below the human level there seems to be no present evidence of intraspecies fighting between large compound groups as competing units. Division of labor between subgroups, especially in relation to food supply and to warfare, has been increasingly important in the history of man. The whole process reaches its climax in civilized, modern man, where millions of individuals are enabled to

fight together with cognizance of a common cause and territory and in whom the foreshortening of time and space by various inventions is rapidly forcing a global organization for the first time in any species.

PHYSIOLOGICAL ASPECTS OF SOCIAL EVOLUTION

The evolution of social life among vertebrates requires, and is made possible by, some reorganization at the physiological level. There is a progressive encephalization of nervous mechanisms which control individual aggressiveness and social behavior among the vertebrates. The basic fighting patterns are organized into a coherent whole below the forebrain level in fish, but mainly by the hypothalamus in the few mammals which have been investigated. Noble (1939) has pointed out that the forebrain mechanisms essential for social behavior have shifted from the corpus striatum of fish and birds to the cerebral cortex of mammals; and, while the influence of the basal ganglia of mammals on social behavior is inadequately known, this statement is evidently true for the most important neural mechanisms of social control. Excessive dependence of aggressive or reproductive behavior on particular sensory modalities, such as vision or audition, is paralleled by increased sensitivity or development of the sensory and central nervous mechanisms concerned (e.g., see Evans, 1938*b*).

Increase in size of well-integrated groups which would facilitate group or tribal dominance requires better memory for individuals and may have been one of the reasons for selection favoring the development of the cerebral cortex in mammals, possibly including early man. The gradual appearance of human intelligence profoundly changed, in some respects, the very rules of evolution for the species *Homo sapiens*. The growth of tradition, including tools, weapons, and language, amounts to the inheritance of characters acquired by direct environmental influence. This does not imply the complete absence of these tendencies below the human level. Rapid social evolution, based on accretion of culture, replaces the comparatively extremely slow organic evolution of subhuman animals. While tradition not infrequently facilitated and was facilitated by success in intergroup conflict, it should be noted that absence of survival value for an individual in battle no longer has very much influence on the elimination or preservation of his ideas.

In the higher vertebrates, dominance orders based on despotism may lead into dominance orders based on leadership as well. While there may be dominance orders not based on despotism in infrahuman vertebrates, especially in some of the higher primates, these do not compare with the great variety of such dominance orders among men which are based on appreciation of special abilities, training, advantages, or prejudices, all in relation to special objectives. To a certain extent, the more primitive forms of competition have merely been replaced by more subtle means of coercion. But self-conscious evolution, combined with the consistent application of scientific method to further our understanding, gives us greatly increased possibilities of control over the less desirable forms of competition.

To summarize, inhibition of aggressive and egocentric competition, increased social tolerance within groups, smoothing of inherited reactions, increased memory for individuals, and better judgment, based on experience, represent contributions of the higher brain levels, and especially of the cerebral cortex in mammals, to harmonious social life of animals in which each individual

tends to recognize, find, and keep its appropriate place. Arbitration and insight into the benefits of co-operation, imaginative powers and profound elaboration of instinctive reactions, language and the capacity for cultural growth, are additional contributions of the cerebral cortex with special reference to the human effort.

RÉSUMÉ

Aggressive behavior plays a major role among vertebrate animals. Competition for food, mates, or territory is frequently based on direct conflict, the intensity of which varies with the shortage of these requirements. When individuals live together as a group and share a common territory, dominance relations tend to become stabilized by habit into a social order of precedence. Such hierarchies intergrade with territorial populations, where distance from the territorial center of individuals does much to determine the order of social dominance. Both types of hierarchies are common in the various classes of vertebrates from fish to man, with the possible exception of the amphibians.

Social rank in the hierarchy is decided by fighting, bluffing, or passive submission at the initial encounter between individuals or during an early series of encounters. Specific tolerances form much of the basis for integration of groups of various kinds of organization, such as the sex pair, family, acquaintanceship group, species, or animal community. Each of these types of group may be integrated to a different degree in different species, and within species the degree of integration varies with intragroup aggressiveness as influenced by the environmental situation, physiological state of individuals, numbers within the group, density and mobility of the species. Classification of vertebrate social groups according to the degree of integration reveals that increase in cooperative aggression by the group as the competing unit is paralleled by decrease in intragroup aggression.

Intraspecies conflict helps to regulate density to an important extent in overcrowded populations, especially by forcing diffusion of the surplus population into suboptimal habitats. Undercrowding is known, for a number of social and infrasocial species, to become dangerous where local numbers of individuals are too few to enable them to form into an effective group for purposes of defense.

The general advantage of groups over individuals as competing units has led to the selection of individuals in terms of social values. Furthermore, competition at one functional level of social organization may be considered as co-operation at a higher level, and vice versa. Co-operation within the group means increased efficiency in intergroup competition.

Examples are cited which indicate that evolutionary trends in aggressive behavior are related in a complex way to evolutionary trends in various social phenomena. Trends in social evolution are paralleled by trends in evolution of physiological adjustments. The most important of these is the progressive encephalization of neural mechanisms of social control with increased subjugation of primitive, more aggressive levels to the control of higher, more social brain levels. Temporary physiological regression may occur at any level of evolution. The most striking fact of endocrine physiology in relation to aggressive behavior has been the persistent association in the vertebrate series of male hormone with aggressive behavior. The appearance of man, with a cumulative social inheritance based on tradition, re-

moved one of the principal impediments to rapid progress in adaptive evolution and also leads to greatly increased possibilities with respect to the effectiveness, control, or elimination of excessive and harmful aggressiveness.

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NEW BOOKS IN PHYSIOLOGICAL ZOÖLOGY

[This section comprises reviews of selected new books containing new and significant material in the field of physiological zoölogy. Books submitted for review should be sent directly to the review editor: Frank A. Brown, Jr., Department of Zoölogy, Northwestern University, Evanston, Illinois.]

AUTONOMIC REGULATIONS[1] BY ERNST GELLHORN

Reviewed by R. W. GERARD
University of Chicago

IN THE last half-dozen years Gellhorn and his collaborators have published some eighty papers dealing with various aspects of autonomic regulations. This monograph is basically a presentation and interpretation of these researches; published and unpublished figures from his laboratory, for example, constitute all but a dozen of the eighty-odd illustrations. This is not to say that relevant work has been neglected; the Bibliography of over eleven hundred titles indicates a wide coverage. Even so, in such an extensive territory, a considerable selection of references has been exercised. Chapters ix, on nervous regulation of the hypophyseal hormones, and xvi, on organismic physiology, are perhaps most completely devoted to analysis of literature.

This is a good book, especially for professional physiologists. It is well organized and clearly presented, without excessive detail, yet mostly with enough description of experiments to enable the thoughtful reader to appraise the factual conclusions drawn from them. The facts, as marshaled, are similarly gathered into interpretations and broader generalizations which flow smoothly from them. This logical pyramiding is at once a strength and a weakness. It gives coherence to the mass of material in widely diverse fields—a coherence which is enhanced in the presentation by the inclusion of chapter summaries and of page cross-references—but it also, necessarily, renders the superstructure insecure in proportion as the underlying facts and arguments can be questioned.

Many such questions can be raised. Gellhorn distinguishes sharply, for example, between simple anoxia and asphyxia (anoxia plus hypercapnia). Anoxia progresses into asphyxia by virtue of progressively impaired circulation, ventilation, and the like. Yet the problem is not considered of how excess CO_2 can accumulate in a tissue supplied with diminished amounts of O_2. He argues that low O_2 depresses metabolism (as witnessed by a fall in body temperature, although CO_2 excess, also claimed to lower metabolism, does not lower temperature) and himself shows that hypoglycemia leads to a lowered blood CO_2. Why, then, should not CO_2 production be lowered roughly in parallel with the O_2 supply? Along similar lines much is made of a synergy between hypoxia and hypoglycemia in decreasing brain oxidations. Yet this is certainly contrary to the immediate expectation that, when a substrate deficit already exists, less oxygen would be used to burn it and that a

[1] New York: Interscience Press, 1943. Pp. xii+373+80 figs. $5.50.

moderate hypoxia would therefore be unimportant. Nor is the problem to be resolved by an indirect sugar mobilization via orthosympathetic stimulation, for anoxia is but a weak stimulus for this.

Chapter XII is devoted to the thesis that somatic nerve centers are depressed, while sympathetic centers in the central nervous system are stimulated, by CO_2 excess or O_2 deficit. It is inherently improbable (although, of course, possible) that such a sharp qualitative difference in the reaction of various neurones should occur and would seem to demand especially direct evidence. Yet one of the very figures (No. 45) showing the failure of a somatic reflex during hypoxia also shows an increase preceding the failure. And a considerable body of evidence for this sequence of early excitation followed by depression is ignored—e.g., the convulsions manifested by an animal poisoned with cyanide. Perhaps sympathetic centers are less responsive than somatic ones, so that a degree of blood change which carries the latter through excitation to depression leaves the former at the excitation phase. Such arguments as the following are also not very convincing: "Since the centers involved in the linguo-maxillary reflex and in the control of blood pressure and respiration are all in the brain stem, it is hard to conceive that the inhibitory influence of higher centers may be different on various brain stem centers." Then follows: "The increased reactivity of the autonomic vasomotor and of the respiratory center to anoxia is due to their reflex stimulation from the chemoreceptors, but the latter have no effect on the center of the linguo-maxillary reflex" (p. 168).

The book is divided into several sections: a brief one on the anatomy and physiology of the autonomic system; a detailed one on circulatory and respiratory adjustments to changes in blood O_2, CO_2, sugar, and volume; a useful survey of autonomic endocrine relations, with emphasis on the hypothalamic control of the hypophysis and on the sympathetic-adrenal and vago-insulin systems; and one on autonomic and somatic nervous-system integration. The fifth section, "Results and Applications," partly applies the material presented earlier to such problems as the total integration of the organism, adrenalin shock, general and spinal anaesthesia, and, especially, schizophrenia.

This insanity, Gellhorn concludes, is directly due to a deficiency of orthosympathetic activity and responsiveness and to relative parasympathetic overaction. The various therapeutic maneuvers which have proved successful have in common only their ability to arouse the orthosympathetic. This conclusion would be more impressive if some vital dyes and other orthosympathetic stimulants were effective rather than ineffective and if noneffective therapies were shown not to stimulate the orthosympapathetic system—if, indeed, anything whatever fails to have an action on it.

The main specific contribution of the volume, in this reviewer's opinion, is in focusing attention on the parasympathetic discharges, which often accompany, but are masked by, the orthosympathetic ones in emergency conditions. A real general contribution is also made by the marshaling, in various logical frameworks, of much information about the ubiquitous and important autonomic system. There is a rich supply of mental food in this volume; it should be chewed before being swallowed.

BEHAVIOR AND NEUROSIS,[1] BY JULES MASSERMAN

Reviewed by CALVIN P. STONE
Stanford University

THIS is an experimental psychoanalytic approach to principles relating to animal and human behavior, particularly to affective, emotional, and psychoneurotic behavior. In chapter i the reader is introduced to a heterogeneous array of topics and viewpoints bearing directly or indirectly on the subject of dynamic psychology. The most important undertaking is that of reformulating certain tenets of Freudian psychology, relating to fundamental needs, in psychobiological terms of a kind that will provide a framework for infrahuman, as well as human, experiments in dynamic psychology. Freudian metapsychology is considered to be deficient in psychobiological orientation, particularly in animal psychology. This is an unfortunate limitation, which should be corrected by competent experimentalists who have an understanding of Freud's dynamic psychology.

After stating some of the more important psychoanalytic tenets, the author formulates four dynamic principles which should link his own animal experiments with these fundamental psychoanalytic concepts and at the same time unify the current literature on experimental neuroses. The four principles pertain to motivation, the adaptive nature of responses, substitutive or symbolic actions, and the vicissitudes of behavior. This introduction is adequate, but not without minor flaws. For example, Jacques Loeb is linked with Driesch as a vitalist, and Herbert Spencer is said to have "revived the Aristotelian science of comparative psychology and laid the principles of modern psychobiology." Neither is in accord with orthodox historical viewpoints. Also, without giving specific citations, he criticizes adversely Pavlov's early work on conditioning for ignoring the role of motivation in the formation and maintenance of conditioned responses. The reader is given an impression of malicious disregard of the corrective suggestions offered by Pavlov's assistants. This criticism is too strong if one evaluates fairly the translated works of Pavlov.

Chapter ii describes apparatus and methods employed in new researches on neuroses to be reported in the monograph. The apparatus is a compact unit which provides confinement for cats or small dogs without recourse to tethers, harness, or stanchions. Within are movable partitions suitable for obstructing the way to the food box or reducing the dimensions of the box. There is a floor grid that can be electrified by the type of electric unit employed by agriculturists to electrify fence wires. Attached outside and within are necessary instruments for presenting symbolic stimuli which the animal must associate with food, painful stimulation, etc. An automatic vendor delivers a standardized piece of food into a box that is covered by a hinged lid. Entering from one side is a tube for delivering an air blast across the food box or onto the animal as it lifts the lid or partakes of the lure. The glass walls of the box make cinema recordings feasible when this is desired. Conspicuously absent are attachments for recording pulse rate, breathing, reflex actions, and movements of head or

[1] Chicago: University of Chicago Press, 1943. Pp. xv+269+7 pls. $3.00.

appendages. These measurements are not highly prized by the author, who, because he is interested primarily in total responses, recorded gross movements such as approach, retreat, vacillation, immobility, stereotyped mannerisitic acts, and movements suggestive of placidity, frustration, fear, and anxiety states.

The description of methods in this chapter is found wanting in details, from both a reader's and an experimenter's viewpoint. Omitted (or possibly given out of place) are such essential items as tank pressure and type of noise made by the air blast; strength of current activating the grid and the condition of footpads of the animal; ages and previous and repeated uses of subjects in this study (if any); provisions for taming or for overcoming timidity from mishandling by caretakers, poundmen, or others unmindful of the ultimate uses they might serve. He has not described, enumerated, or illustrated either the total routine or the special records made on individuals in each group of animals.

Chapter iii is a reprinting, without alteration of conclusions, of a 1941 monograph, published in *Psychosomatic Medicine*, on the role of the hypothalamus in emotion. To the original monograph have been added only a brief introduction and minor emendations. The author voices and supports the hypothesis that the hypothalamus neither mediates nor governs the expression of affective or emotional experiences in animals (somewhat less certain regarding man), although it may integrate and reinforce efferent neural impulses "controlling some of the sympathetic and motor manifestations of fear and rage." His own experimental contributions to the problem are a substantial contribution eminently worthy of careful examination and serious study.

Chapter iv presents new data on experimentally aroused neuroses in cats and dogs. In all, eighty-two cats and two dogs were used. He found a great many types of learning problems, some involving severe frustrations, which were unproductive of neurotic behavior. But the latter could be induced readily in cats by the use of the air blast directed across the lid of the food box or onto the animal as it was about to eat. Neuroses also could be induced by grid-shocks, or by a combination of these two annoying stimulus situations. The neurotic reactions consist of change in spontaneous activity, phobic responses to feeding signals, counterphobic behavior patterns, regressive reactions, and preoccupations with substitute satisfactions. He found that the following conditions alleviate maladjusted behavior: (1) periods of rest from conflict-provoking situations; (2) diminution of strength of hunger by prefeeding; (3) reassurance and persuasion by petting; (4) forced solutions of problems when inhibitions stood in the way of success; (5) social facilitation by use of a stable, problem-wise cage-mate; and (6) allowing the animal partial control of the situation by giving him some essential part to manipulate at will.

The author's methods of presenting results in chapter iv fall short of what an experimentally oriented reader expects. There are illustrative cinema shots, chosen excerpts from descriptive protocols, and didactic generalizations. But the reader does not know whether the author is describing run-of-the-mine cases or merely selected instances which typify preconceived categories of behavior, based on reformulated Freudian mechanisms. As every experimenter knows, clinical records are among the most difficult to compile without confusion of observations and imputations or

inferences. It is the reviewer's opinion that neither his case records, his analyses, nor his interpretations measure up to the standard set by Adams in his monograph on the cat more than a decade ago. Nevertheless, the chapter should be experiment-provoking because of its innovations in method and the current wave of heightened interest in neurotic behavior in animals.

Part II, consisting of five chapters, reviews selected behavioral studies on the cat as an experimental animal, conditioned reflex concepts of behavior and neurosis, motivation of behavior, behavioral consequences of frustration and conflict, and "social interaction" as related to neurosis. These are good reviews which should prove to be exceedingly valuable to those who do not follow regularly the periodical literature in this area of comparative psychology.

Part III is composed of two short chapters dealing with conditioned reflex concepts as related to psychoanalysis and to infantile habits and attitudes. It closes with a brief résumé of the therapeutic principles developed in the preceding chapters and their bearing upon the cause and cure of neurotic behavior.

The monograph as a whole will interest psychobiologists who endeavor to keep abreast of active trends in dynamic psychology. Psychiatrists and psychoanalysts desiring to make an initial contact with comparative psychology will find this monograph informative and thought-provoking. And, without wishing to be facetious or unreasonable, may we express the hope that it will cause some portion of the current wave of experiments on animal neuroses to be directed to *Felis domestica*, thereby providing a much-needed diversion from the lowly, overworked laboratory rat.